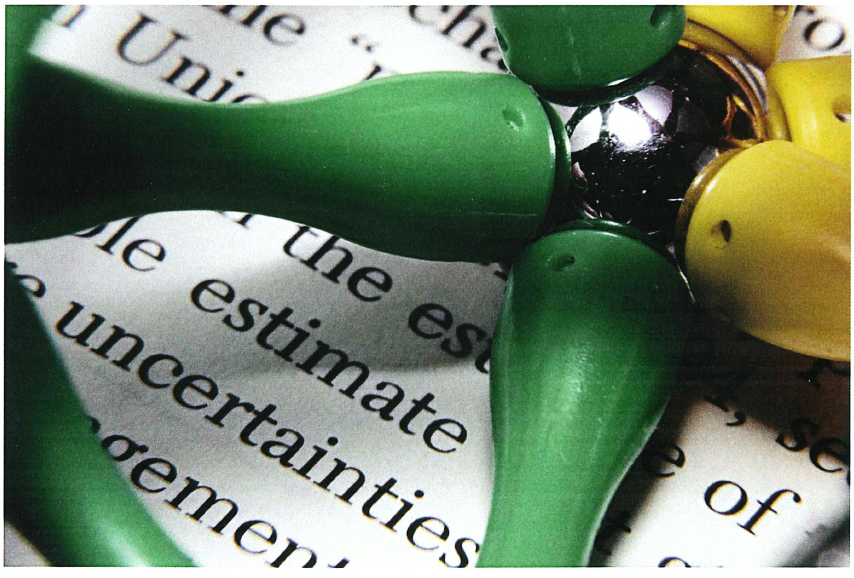
Acta Universitatis Agriculturae Sueciae

Doctoral Thesis No. 20012:22
Faculty of Natural Resources and Agricultural Sciences

Population Viability Analysis under Environmental Change

Development of Bayesian Tools

Alejandro Ruete



Population Viability Analysis under Environmental Change

Development of Bayesian Tools

Alejandro Ruete
Faculty of Natural Resources and Agricultural Sciences
Department of Ecology
Uppsala

Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2012

Acta Universitatis agriculturae Sueciae
2012:22

Cover: Metaphoric image describing observable and hidden variables present when estimating uncertainties.
(photo: A. Ruete)

ISSN 1652-6880
ISBN 978-91-576-7658-0

Print: SLU Service/Repro, Uppsala 2012

Population Viability Analysis under Environmental Change: Development of Bayesian Tools

Abstract

An understanding of the links between population dynamics and environmental variability, combined with information on how these factors change over time, is necessary to understand and predict population dynamics and viability in changing environments. Scientists need also to acknowledge uncertainties in their understanding of systems, which is straightforward using Bayesian statistics. This allows us to know with more certainty, although it sounds contradictory, how a biological system works.

First, the hierarchical model developed in paper I illustrates how conclusions and decisions to be made based on population viability analysis could be dangerously misleading if uncertainties are not taken into account. The probabilistic long-term growth rate parameter, log λ_S, is estimated for the first time, and I discuss a new way to interpret this parameter. Based on simulations done with this model, we stress in paper II that ignoring relevant uncertainty sources generally gives an unwarranted impression of confidence in the results. The procedure used in this work increased our understanding of the relative importance of different uncertainty sources, and helps choosing which sources to include when evaluating the impact of climate change.

Second, the modelling approach developed in paper III allows us to estimate colonization rates of non-equilibrium metapopulations. It reconstructs a time series of the most likely colonization events leading to the observed pattern of occupied and non-occupied patches. It requires only snapshot data on the occurrence pattern, as well as data on patch ages and on the landscape history. In this case I stress how the choice of a modelling approach has important implications on metapopulation viability analysis.

I finally draw conclusions on the methodological advances achieved, and on the implications for the conservation of the study species. Using Bayesian statistics both process uncertainty, and parameter uncertainty and variability are captured, and predictions are turned into a probabilistic statement that is useful for management. Uncertainties are no longer an obstacle, but a mandatory aspect to include in population viability analysis.

Keywords: climate change, epiphyte, epixylic, fragmentation, habitat loss, hierarchical model, lichen, metapopulation dynamics, moss, population dynamics, PVA, uncertainty

Author's address: Alejandro Ruete, SLU, Department of Ecology,
P.O. Box 7044, 750 07 Uppsala, Sweden
E-mail: Alejandro.Ruete@slu.se; aleruete@gmail.com

Dedication

To my beloved Celina and Clara, without whom these pages would have no meaning.

“I know that I know nothing.”
Socrates

Contents

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

I Ruete A., Wiklund K., and T. Snäll (2012). Hierarchical Bayesian estimation of the population viability of an epixylic moss. *Journal of Ecology* 100(2), 497-507.

II Ruete A., Yang W., Bärring L., Stenseth N.C., and T. Snäll (2012). Disentangling effects of uncertainties on population projections: climate change impact on an epixylic bryophyte. *Proceedings of the Royal Society Biological Sciences Series B* (early view).

III Ruete A., Fritz Ö., and T. Snäll. Estimation of colonization rates of non-equilibrium metapopulations based on patch ages and landscape history. (manuscript).

IV Ruete A., and T. Snäll. Effects of forest protection and management scenarios on epiphyte metapopulation viability. (manuscript).

Papers I and II are reproduced with the permission of the publishers.

The contribution of Alejandro Ruete and co-authors to the papers included in this thesis was as follows:

I Main author, field work, and analysis. Design and idea together with Tord Snäll. Karin Wiklund designed and conducted the field work in 1996-2003.

II Main author and analysis. Design and idea together with Tord Snäll, Lars Bärring, Wei Yung and Nils Chr. Stenseth.

III Main author, field work, and analysis. Design and idea together with Tord Snäll. Örjan Fritz designed and conducted the survey on the study species.

IV Main author and analysis. Design and idea together with Tord Snäll.

Abbreviations

CBD	Convention on Biological Diversity
GCM	Global Climate Model (a.k.a. General Circulation Model)
HPDI	Highest Probability Density Interval
IPCC	Intergovernmental Panel on Climate Change
PPD	Posterior Probability Distribution
PVA	Population Viability Analysis
RCM	Regional Climate Model
SRES	Special Report on *Emission Scenarios (*greenhouse gases)

Mature sporophyte of *Buxbaumia viridis*, growing on decayed Norway spruce (*Picea abies)* dead wood. Photo: A. Ruete

1 Introduction

"*I know that I know nothing*". Socrates meant that one cannot know anything with absolute certainty but can feel confident about certain things. Regardless of any philosophical connotation, scientists need to acknowledge uncertainties in their understanding of systems. In ecology, living systems are far from behaving in a simple fashion or being easily predictable. However, with the rise of more powerful computation capabilities and using an old probabilistic theory (Bayes' theorem; Bayes & Price, 1763), it is now straightforward to acknowledge uncertainties. This allows us to know with more certainty, although it sounds contradictory, how a biological system works. For example, uncertainties can now be integrated throughout the models that describe the fluctuations of populations' abundances, and we can retrieve probabilities for all possible outcomes given known or assumed environmental conditions. Conservation biologists can now attach true probabilities to statements about the long-term viability of populations. Throughout this thesis I will show that uncertainties are no longer an obstacle, but a mandatory aspect to include in population viability analysis.

1.1 Population Viability Analysis

Population viability analysis (PVA) is the process of identifying the threats faced by a species. It entails the evaluation of data and models to anticipate the likelihood that a population will persist for some arbitrarily chosen time into the future (Beissinger & McCullough, 2002; Morris & Doak, 2002). There is no single recipe to follow when doing a PVA, because each case is different in so many aspects. PVAs vary based on the ecology of the species, the expertise of the modellers, and the amount of data available (Beissinger & McCullough, 2002; Morris & Doak, 2002).

PVA holds to the assumption that the bigger the population (or metapopulation) the larger the chances for the population to persist, i.e. higher viability (Hanski & Ovaskainen, 2000; Beissinger & McCullough, 2002). It also embraces the estimation of a minimum viable population and the time to extinction. The uncertainty and utility of the two later parameters have been largely discussed (Brook *et al.*, 2002). Alternatively, PVAs are recommended to be used in a comparative –relative– way to evaluate the effectiveness of different management options. Because of this it has been argued that PVA predictions do not need to be precise (Brook *et al.*, 2000, 2002). However, there is no clear dichotomy between relative and absolute predictions, and the accuracy of PVA is not necessarily low.

PVA is often oriented towards the conservation and management of rare and threatened species, with the goal of applying the principles of population ecology to improve their chances of survival (Akçakaya, 2000). Threatened species management has two broad objectives. The short-term objective is to minimize the risk of extinction. The long-term objective is to promote conditions in which species retain their potential for evolutionary change (Akçakaya, 2000). Within this context, PVA may be used to address three aspects of threatened species management:

1. Planning research and data collection. PVA may reveal that population viability is insensitive to particular parameters, therefore simpler models with less data could be fitted.
2. Setting policies and priorities for allocating scarce conservation resources.
3. Ranking management options, and predicting the likely response of species to scenarios of environmental change.

To develop a model for PVA we need to combine existing information into predictions about the persistence of species under different conservation and management scenarios (Beissinger & McCullough, 2002). The structure of the model and the questions to be addressed usually determine how the results will be presented. In most cases, the model will include stochasticity, which means that the results should ideally be presented in probabilistic terms.

Population models can inform us about the trend and long-term viability of populations. A suitable and commonly used estimator of population trend and long-term viability is the stochastic growth rate, $\log \lambda_S$ (Lewontin & Cohen, 1969; Tuljapurkar & Orzack, 1980). This parameter accounts for the effect of inter-annual variation in population size on population viability. It can be compared to a threshold, e.g. if $\log \lambda_S$ is <0, the population is bound to decline, while if it is ≥ 0, the population is viable. However, this parameter should not be understood as a general exponential growth rate of the population. I discuss

and elaborate further on different ways to estimate and interpret this parameter in 4.1.

Alternatively, risk curves (Akçakaya & Sjögren-Gulve, 2000; figure 7), or probabilities of viability improvement (figure 10), provide a convenient way of presenting results of PVA simulations. The risk curves give the risk of decline of a population as a function of the amount of decline, and allow comparing with a reference scenario. The probabilities of viability improvement give the probability that, after a given time, the viability of a population has increased compared to a reference scenario.

1.1.1 Bayesian Population Viability Analysis

"*Uncertainty is just about the only certainty in PVA*" (Beissinger & McCullough, 2002). How we deal with uncertainty in making decisions with PVA models is the subject of much on-going work (e.g. Araújo *et al.*, 2005; González-Suarez *et al.*, 2006; Bakker *et al.*, 2009; Devenish Nelson *et al.*, 2010; McClintock *et al.*, 2010; Gillespie *et al.*, 2011). Most PVA methods rarely incorporate parameter uncertainty, although such uncertainties are often very large in ecological data (Wade, 2002). Uncertainties lay in the natural variation of the actual process modelled in the projection, and in the imperfect knowledge of the parameter values and starting conditions. Accounting for uncertainties means that one acknowledges that parameters are not deterministic, and that nature is variable. PVA models are often complex trying to capture all important risk factors, but at the same time they often fail to properly account for uncertainty and variability. PVAs that ignore uncertainty can be misleading and inaccurate (I, II).

Using Bayesian statistical approaches in PVA is an alternative to frequentist statistics that offers a way to incorporate uncertainty into model building (Wade, 2002). Frequentist statistics (a.k.a. "statistics") is by far the most widely used –and taught– approach for statistical inference among ecologists. However, Bayesian statistics has gained increasing support in the last decades (Ellison, 2004).

Any data can be analysed with techniques from either approach. However, there are some fundamental differences between these two approaches. Inference in frequentist statistics is made by estimating the "true" value of parameters (a mean) and its confidence limits, and calculating a probability (*p-value*) associated with a specific hypothesis test. Frequentist statistics never leads to probability statements about the values of parameters, but to a statement about the probability of observing specific data, given values for parameters. Hypotheses can only be rejected with certainty, which then lead our "belief" towards an alternative hypothesis. Strictly, if not rejected, not

much can be said about tested hypothesis (Popper, 1963). Bayesian statistics differ in that inference is made from statements about the probability of different parameter values given the observed data and prior knowledge on the parameter. Parameter estimates constitute a probability distribution, the posterior distribution. In this approach, data serve as evidence to support an hypothesis, rather than testing it (Ellison, 2004).

Formally, only Bayesian statistics results in probability statements about the possible values of parameters (Goodman, 2002). Frequentist confidence intervals are sometimes wrongly interpreted as a probability distribution of the parameter, although this mistake has been pointed out long ago (Berger & Berry, 1988). The confidence limits are calculated from the sampling distribution centred on the point estimate. This distribution describes the probability of observing various data, given the true parameter is exactly equal to the point estimate. In contrast, a Bayesian interval, termed a credible interval or highest probability density interval (HPDI) has a probabilistic interpretation. The estimated posterior distributions can be characterized by different statistics, e.g. the most likely value for the parameter, the mode, can be identified. Bayesians can make statements like: "there is a 95% probability that the true parameter value is within this interval" (figure 1a) or "there is a 50% probability that the true parameter is smaller than a critical value x" (figure 1b; Wade, 2002; Ellison, 2004), while frequentists cannot. Even more, it is possible to compare probability distributions among each other, e.g. reporting the probability of one distribution being higher than another (figure 1c).

Figure 1. Interpretations of posterior probability distributions. a) mode, indicated with a diamond, and HPDI, indicated with thick and thin segments; b) proportion below (or above) a critical value "x"; c) comparison of posterior probability distributions.

One of the features of a Bayesian model is that it provides posterior probability distributions, given the data and *à priori* knowledge about the parameters. Prior information about a parameter can be based on independent data or expert opinions. The modeller may also have vague prior knowledge about the parameters, and technically this is implemented as uninformative (flat) prior

probability distributions for the parameters. Also, the Bayesian framework allows a relatively easy estimation of missing observations based on existing observations and model parameterisation (Gelman *et al.*, 2004).

Simulations based on Bayesian posterior distributions of model parameters can account for, and propagate natural variability and uncertainty, while simulations based on parameters estimated by frequentist methods do not. Inferences and predictions about population dynamics require proper accommodation of environmental variability and data uncertainty on different temporal and spatial scales (Clark & Bjørnstad, 2004). The hierarchical Bayesian framework allows accounting for different sources of variation across different temporal and spatial scales in population models (Ellison, 2004; Gelman *et al.*, 2004; Clark, 2005).

Bayesian approaches open the door for parameter uncertainty to be directly incorporated into a PVA. Under the Bayesian approach, both aspects of the uncertainty in a PVA –process uncertainty, and parameter uncertainty and variability– are captured, turning the prediction into a statement that is useful for management. Uncertainty does not invalidate a PVA. Quite the contrary, correct representation of the uncertainty, in a way that can be interpreted literally as a frequency of outcome, or the odds for a (bad) event to happen under a certain scenario, is exactly what is needed to inform management (Goodman, 2002). Bayesian PVA leads to single probabilities, rather than to estimates of probabilities with associated confidence intervals.

1.2 Environmental Change and Declining Populations

The spatial and temporal variation of the environment affects mean levels as well as variability of population demographic processes, such as survival, recruitment or reproduction (Stenseth, 1999; Stenseth *et al.*, 2002; Ågren *et al.*, 2008; Morris *et al.*, 2008). An understanding of the links between population dynamics and environmental variability, combined with information on how these factors change over time, is necessary to understand and predict population dynamics and viability in changing environments (Gotelli & Ellison, 2006), and to scale up from local processes to large spatial scales (Jeltsch *et al.*, 2008).

On one hand, weather variation has been identified as a main driver of variation in demographic processes (Lima *et al.*, 2001; Stenseth *et al.*, 2002; Jönsson *et al.*, 2009), and the population size of some species even track weather variability (Jongejans *et al.*, 2010). A change in the balance between climatic variables may lead to a decline of many species. Moreover, both the mean and the variability of climatic variables are changing (IPCC, 2007).

Often, climatic variables have opposite effects on species population growth, and it is therefore difficult to anticipate the future trend of populations without making simulations where the population dynamics are driven by predictions of e.g. future temperature and precipitation (e.g. Snäll *et al.*, 2009; paper II).

On the other hand, the environment (apart from weather) is often highly variable at the scale individuals perceive it. Many populations live in "patchy" landscapes, and their population dynamics can be generalized by the metapopulation theory (Hanski & Gaggiotti, 2004). Due to severe habitat loss and fragmentation, many populations that earlier experienced continuous landscapes are now structured in space as metapopulations (Hanski & Gaggiotti, 2004), and may function as such. Because habitat loss usually involves habitat fragmentation, the connectivity between occupied and empty habitat patches plays a major role in studies of habitat loss. For habitat specialists, especially those with a relatively poor colonizing ability, habitat fragmentation results in a reduction of connectivity and in reduced colonization rates (Hanski, 1999; Hanski & Ovaskainen, 2000). Moreover, in changing landscapes species distributions are likely to lag behind habitat changes, and are hence not in equilibrium with the current landscape structure. Species extinctions after habitat decline may be delayed, which defines the extinction debt (Tilman *et al.*, 1994). Extinction debt can either be paid by allowing the species to go extinct or by improving the landscape structure before the species have gone extinct (Hanski & Ovaskainen, 2002). We need to know whether a species is likely to persist in a landscape that has undergone severe habitat loss, and which management options will improve current situations. Adding and expanding protected areas is indeed a way of increasing connectivity (Noss, 1983; Götmark & Thorell, 2003; Hanski, 2011; but see Hodgson *et al.*, 2009). The Convention on Biological Diversity (CBD) proposes a target of protecting at least 17% of terrestrial ecosystems (Convention on Biological Diversity, 2010). However, high habitat quality in non-protected areas, improved by means of complementary [1] conservation strategies also improve landscape connectivity, protected areas' performance and species persistence (Margules & Pressey, 2000; Pressey *et al.*, 2007; Hodgson *et al.*, 2009; Primack, 2010; Olds *et al.*, 2012). Complementary conservation strategies include, but are not restricted to, alternative ways of performing economic activities in non-protected areas, such as retention actions in forestry, or hedgerow protection in agriculture.

Our ability to anticipate future population changes is of great concern, particularly under the fast rates of change that humans are imposing on ecosystems (Clark *et al.*, 2001). Therefore, assessing long-term population

[1]. Complementary to the strategy of setting aside protected areas.

viability and testing for species persistence under different scenarios of climate change or landscape management may require simulations based on models that account for uncertainty and variability.

1.3 Taxonomic Knowledge Gap

Briefly, but not least important, I want to point out the importance of researching on the ecology and conservation of cryptogamic species, i.e. algae, lichens, mosses and ferns. Even during conservation meetings, I have often been asked or heard questions like "What is a lichen good for?" or "What is the conservation value of a moss?". Evidently, there is a gap not only in people's perception of the value of these species, but also on the literature (Fazey *et al.*, 2005; Lawler *et al.*, 2006). Often, they are not even mentioned in reviews (see Lawler *et al.*, 2006; Parmesan, 2006). Although not as abundant as for other taxa, the existing literature supports the key role these species have in ecosystem processes (Jonsson *et al.*, 2005; Økland *et al.*, 2009; Granath *et al.*, 2012), as indicator species (Nilsson *et al.*, 1995; Hedenås & Ericson, 2000; Gignac, 2001), and how they constitute a large proportion of the biodiversity of many biomes (Gignac, 2001). Given the expected readership of this thesis, I think it is not needed to mention the intrinsic conservation value of any species (Primack, 2010). This work explores both the ecology and conservation of some cryptogams.

1.4 Do We Need More PVA Tools?

"*Essentially, all models are wrong, but some are useful*" (Box, 1976). To realize when a modelling framework is not useful for PVAs, when we need to build upon old frameworks, and when a new framework should be developed is of major importance. I think that when modelling population dynamics it is better to include key processes with large uncertainties, than to include numerous details and failing to properly describe key processes. While complexity is not always necessary to consider, good knowledge of the processes is absolutely needed.

With the development of new computation capabilities new doors have been opened for a better understanding of biological processes, and for better estimation of population viability. Anthropogenic rates of change imposed to the environment may bring along challenges to the way systems are studied. We need to know what to expect after these rates of change, and how to revert unfavourable scenarios. For some problems we simply need to build upon old theories and methodologies. In this case we may need new interpretations of

parameters (I). For some others we need new ways of thinking that lead us to new estimates (III) and maybe to new theories.

The developing capacity for prediction requires careful model evaluation, which can involve model selection, model averaging, or both. Model selection methods are routinely used in ecological applications (Clark *et al.*, 2001; Burnham & Anderson, 2002). Because the models themselves are often uncertain, ecological forecasting may eventually rely more heavily on model averaging. In these cases we need to average models (I, II), as no particular model is substantially more adequate to the data. However, Knutti (2010) proposes that we should give different weight to independent models, meaning "*the end of model democracy*". In more extreme cases, there is no room for averaging and we need to select the model that is most biologically reasonable (III, IV). There is no need for a radical position. The approach to take is problem-specific, and depends on the ecologist judgement. However, precaution is needed as the model choice has direct implications on PVA, on decision making, and hence on conservation.

Uncertainties Throughout Scales

It is a challenge to disentangle the relative importance of environmental drivers at different spatial scales on the inter-annual variation in population abundance. While processes driving inter-annual variation in abundance may act at regional scales, organisms also interact with each other, and with their substrate at local scales (Ovaskainen & Cornell, 2006). It has even been shown that variation in local conditions can buffer the population response to regional weather variation (Davison *et al.*, 2010).

Different approaches have been used to model population dynamics driven by regional and local processes. Autoregressive models are widely used to analyse population time series by statistically linking the population autocorrelation with environmental variability (Royama, 1992; Inchausti & Halley, 2003; Stenseth *et al.*, 2004). This approach, however, makes it difficult to separate a lagged density-dependent structure of the population from a lag in the response to the environmental variability (Turchin & Berryman, 2000). Another approach is mechanistic demographic matrix modelling (Caswell, 2001), which has recently become complemented with sub-models for the relationship between the demographic parameters and environmental variables (Keith *et al.*, 2008; Davison *et al.*, 2010; Hunter *et al.*, 2010; Toräng *et al.*, 2010). Coulson *et al.* (2008) even combined these approaches by averaging age-specific survival and recruitment rates in the estimate of the population growth rate, and allowing this relationship to vary more realistically over time.

The hierarchical Bayesian framework properly accounts for and propagates environmental variability and data uncertainty at different scales on inferences and predictions about population dynamics (Clark & Bjørnstad, 2004; Clark, 2005). This approach has been suggested to model the effect of environmental variability on the rates of population or metapopulation dynamics (Goodman, 2002), and it has recently been applied to the demographic modelling approach to estimate demographic parameters, e.g. the reproductive rate (Evans *et al.*, 2010), and to model population or metapopulation dynamics (Bull & Bonsall, 2008; Snäll *et al.*, 2008).

Obsolete Estimates of Population Viability

As mentioned in 1.1, the stochastic growth rate, log λ_S is a suitable estimator of species trends and long-term viability (Lewontin & Cohen, 1969; Tuljapurkar & Orzack, 1980). Methods exist to estimate the effect of variability in demographic processes on the stochastic growth rate and its uncertainty (Caswell, 2001; Evans *et al.*, 2010; Hunter *et al.*, 2010). However, PVAs from point estimates are obsolete. The Bayesian approach adds a fundamental aspect to the population viability estimate: natural variability, as well as process and sampling uncertainty across scales (Clark & Bjørnstad, 2004; Clark, 2005). This approach allows the stochastic growth rate to be estimated under all possible combinations of observed environmental variability. At the moment of writing this thesis, I was not aware of any estimate of the full probability distribution of log λ_S in which the variability across spatial scales was accounted for, and where this distribution was contrasted with estimates based on other methods.

Sources of Uncertainty

We need to understand the influence of different sources of variability and uncertainty on population dynamics, to confidently rely on the statements made from population projections, especially when combining climate models and a population dynamics model. In projecting population changes into the future, it is important to account for the relevant sources of uncertainty to provide a robust picture for evaluating risks (Clark *et al.*, 2001; Snäll *et al.*, 2009; II). This means accounting for the joint effects of climate and ecosystem variables, and using up-to-date modelling techniques that allow proper treatment of uncertainties (Clark *et al.*, 2001). In this way, we can quantify the overall projection uncertainty that arises from interactions among model formulations, parameter estimates and their inherent uncertainties (Clark *et al.*, 2003; Higgins *et al.*, 2003).

The influence of climate model uncertainties has been well-studied by climatologists (e.g. Déqué *et al.*, 2007; Buser *et al.*, 2009; Kjellström *et al.*, 2011; Nikulin *et al.*, 2011; Samuelsson *et al.*, 2011), but our understanding of their impacts on projections of biological systems is scarce. Uncertainties could propagate from many parts of the chain global climate model (GCM) – regional climate model (RCM) – population dynamics model. The variation in projections by climate models with different approaches for modelling physical processes (model formulation) or different parameter sets (parameterization) are often larger than the variation resulting from the climate scenarios investigated by a specific model (Christensen *et al.*, 2007; Fowler *et al.*, 2007; Tebaldi & Knutti, 2007; Snäll *et al.*, 2009). Averaging over ensembles of climate models accounts for this uncertainty (Collins *et al.*, 2006). Some studies account for the uncertainty in the biological process models (Bellard *et al. in press*; Snäll *et al.*, 2009; Fernández-Chacón *et al.*, 2011; Jönsson & Bärring, 2011), and this has been put forth as the right approach to use (Loehle, 2011). However, none of these studies increase our understanding of how uncertainty sources in climate or ecosystem modelling influence the projections of the biological systems.

Uncertainties in Data but Certainty in Processes

A key problem in studying metapopulation dynamics of many sessile species is their slow dynamics relative to human time scales. This make the metapopulation dynamics of many sessile species difficult to study, and trade-offs between data quantity and quality are needed (Snäll *et al.*, 2003; Öckinger *et al.*, 2005; Gjerde *et al.*, *in press*; Fedrowitz *et al.*, 2012; Johansson *et al.*, 2012). Classical metapopulation models, such as the incidence function model (IFM; Hanski, 1999), have the ability to estimate colonization and extinction rates with data from few or even only one point in time (snapshot data henceforth). This is often a requisite when data from different points in time are lacking (Hanski, 1999), or when events are rare (Keeling *et al.*, 2004). The IFM assume that colonization and extinction rates are balanced (in equilibrium), hence there is an equilibrium in the proportion of occupied patches (Hanski, 1999). Even when there is high patch turnover (i.e. transient patches) the equilibrium assumption can still hold, if the metapopulation dynamics are considerably faster than landscape dynamics. Some modified versions of the IFM have been developed to study metapopulation dynamics on dynamic landscapes by adding the effect of time on it (Verheyen *et al.*, 2004; Hodgson *et al.*, 2009; Johansson *et al.*, 2012).

The equilibrium assumption may, however, be violated in many cases where the landscape dynamics are not at equilibrium –e.g. due to habitat loss

and fragmentation, or due to succession (Hanski *et al.*, 1996). Observed patterns of non-equilibrium metapopulations are largely determined by its history. An understanding of the metapopulation dynamics is therefore very limited (Hanski, 1999; Verheyen *et al.*, 2004; Snäll *et al.*, 2005) or even impossible without reference to its past (Herben *et al.*, 2006). Historical effects often reflect a delayed response to landscape changes, either due to local populations resisting extinction or due to slow colonization when new habitat patches become available (Hanski, 1999; Snäll *et al.*, 2005; Herben *et al.*, 2006). When the landscape has, for example, undergone a long history of habitat loss and fragmentation, current modelling approaches assuming equilibrium may lead into unrealistic (overestimated) estimates of the colonization rate and dispersal kernels. Münzbergová *et al.* (2005) explained current plant distribution patterns based on a mechanistic non-equilibrium metapopulation models coupled with demographic data and landscape history. However, this model cannot be parameterised with only snapshot data. Snäll *et al.* (2005) have developed a non-equilibrium metapopulation model based on snapshot data. However, the effect of the landscape history on the metapopulation could not be evaluated because of the lack of historical data on the host trees. We present an approach that so far has been lacking to parameterize non-equilibrium metapopulation models based on snapshot data and on data on the landscape history.

2 Thesis Aims

The general aim of this thesis was to develop PVA tools capable of accounting for different sources of uncertainty and natural variability, and to propagate them in simulations of (meta)population dynamics. The thesis was based on two study systems (figure 2) to tackle the modelling needs mentioned in 1.4. Both study systems allowed me to develop new methodologies (aims 2, 3, 4 and 6), but also to explore applied conservation questions for the study species (aims 2, 5, and 7).

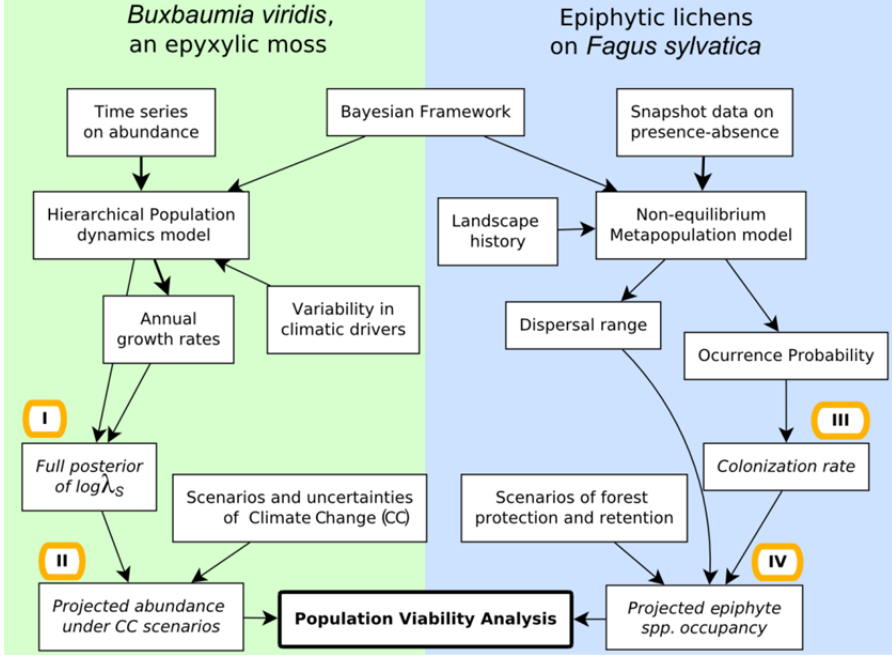


Figure 2. Conceptual organization of the thesis. Roman numbers indicate the paper connected to specific aims

2.1 Specific Aims

1. To develop and evaluate a hierarchical Bayesian model for the population dynamics of species whose dynamics are affected by i) regional processes, e.g. inter-annual variation in seasonal weather regulating the growth rate of the species; and ii) local variables, e.g. preceding year's population abundance or resource amount. (I)
2. To estimate the local long-term viability of *Buxbaumia viridis*, under current environmental conditions based on full probability distribution of the parameter log λ_S. (I)
3. To provide an alternative interpretation of the confidence of log λ_S. (I)
4. To compare the relative importance of different uncertainty sources on the estimate of future population viability, including multiple climate simulations, uncertainty in the biological process, and parametric uncertainty, relative to the variability introduced by different SRES scenarios. (II)
5. To investigate the influence of change on climatic variables (e.g. temperature and precipitation) driving the population dynamics of *B. viridis*. Specifically, what is the probability of decreased population abundance in the future given different scenarios of climate change? (II)
6. To develop a method for estimating the colonization and extinction rates of non-equilibrium metapopulations, using only snapshot data, and data on the landscape history. (III)
7. To assess whether metapopulation dynamics of epiphytic lichens on beech are viable with current international biodiversity protection targets, as well as with implemented complementary conservation strategies. Specifically, do current conservation strategies improve the species viability compared to a scenario with no protected areas nor complementary conservation strategies? (IV)

3 Materials and Methods

3.1 Hierarchical Population Dynamics Model (I, II)

3.1.1 The Epixylic Moss Study System

Buxbaumia viridis (DC.) Moung. & Nestl. (Buxbaumiaceae) is a dioecious moss that grows on strongly decayed dead wood patches in coniferous or broadleaved forests (Nyholm 1979). The gametophyte is minute and difficult to find in the field, while the sporophyte varies in length from 7 to 25 mm (Möller 1923). Little is known about the life cycle of *B. viridis*. In eastern-central Sweden, sporophytes usually emerge in October, and most spores are released in middle June the following year (Wiklund pers. obs.). Based on what is known about the life cycle of the congeneric *B. aphylla* in North America (Hancock & Brassard 1974), it is believed that the life cycle of *B. viridis* is annual or paucennial –capable of completing the cycle in one year or surviving a few years with reduced or arrested growth, depending on weather conditions. A local population persists on a patch of dead wood in the form of either perennial protonema (the first stage in the bryophyte life cycle; Hancock & Brassard 1974), or brood bodies (groups of cells which are specialized for survival under harsh conditions), or by immigration of new individuals by spores. Each persistence form has an effect on different spatial and temporal scales. Since the dead wood patches are temporary (Söderström 1988), landscape-scale persistence relies on recurrent spore dispersal and establishment (Wiklund 2003). *B. viridis* has a circumboreal distribution, but the population size is small wherever it occurs (Hallingbäck 2002). The species is classified as 'Vulnerable' in Europe (European Committee for Conservation of Bryophytes 1995).

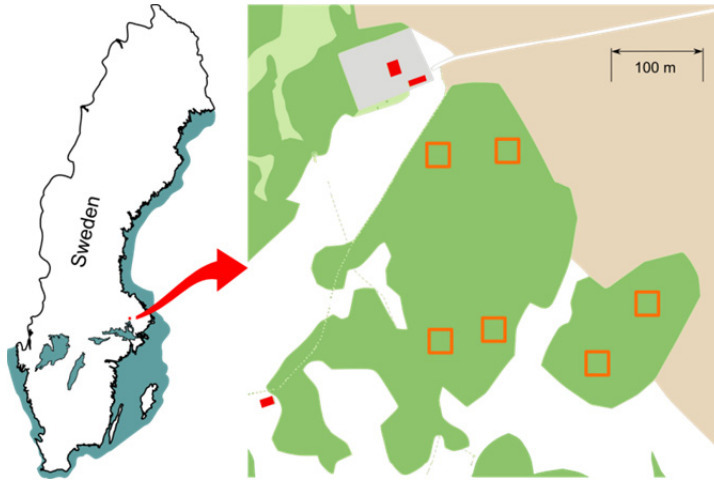


Figure 3. Map over area in Vipängen. Forest is shown in green, and sampling plots are shown as orange squares.

The 7-ha study area is situated in eastern-central Sweden (Vipängen, Uppsala, 59º 49'N, 17º39' E; figure 3). It belongs to the boreo-nemoral forest, is dominated by *Picea abies*, and is surrounded by arable lands and pastures (figure 3).

We used time series on mature sporophytes abundance (observed in June) for 1996-2003 and 2008, and data on the amount of dead wood for 1995 and 2008, from six 25 × 25 m permanent plots. We aimed at sampling the variation in density of occupied dead wood patches. The data from 2008 were utilized for model evaluation.

We obtained daily precipitation and temperature data for the period 1995-2008 from the Ultuna weather station, located 100 m north of the forest. The weather data were summarized as the number of days with temperatures below 0 ºC for the period October to November, sum of precipitation (mm), and mean of monthly temperature means (ºC) for the period March to June (autumn frosts, spring precipitation and spring temperature, respectively). These variables were believed to be critical in the species life cycle, since sudden freezing spells in autumn may cause high mortality of immature sporophytes (Hancock & Brassard, 1974), and water stress in spring may reduce the survival of the sporophytes in the maturation phase (Wiklund & Rydin, 2004).

3.1.2 The Model

The time series on abundance of mature sporophytes allowed us to develop a hierarchical model for the yearly abundance of *B. viridis* sporophytes as a function of local and regional conditions. I next describe the final model

resulting from a selection procedure. The full model is described and discussed in detail in paper I, including details on a submodel on deadwood amount which is not included in the final model and therefore not discussed here.

The deterministic skeleton of population regulation took the form of an underlying exponential population growth model, which is reasonable for bryophytes (During, 1979). We linearized the model and applied the hierarchical generalized linear modelling framework (Gelman & Hill, 2007): we assumed that the local-scale (i.e. plot-level) abundance of sporophytes followed a Poisson distribution with mean $\mu_{y,p}$, specifically,

$$N_{y,p} \sim Poisson(\mu_{y,p}), \quad \text{eqn 1}$$

where,

$$\log \mu_{y,p} = \log \lambda_y + \beta_1 \cdot \log\left(N_{y-1,p} + 10^{-3}\right) + \varepsilon_{y,p}, \quad \text{eqn 2}$$

where $N_{y,p}$ is the observed abundance of sporophytes in year y in plot p, and λ_y is the regional, year-specific population growth rate, which was modelled further as a function of weather (equations 3 and 4). $N_{y\text{-}1,p}$ is the observed abundance of sporophytes in the preceding year. The 'effect-size' parameter β_1 determines the proportion of spores produced by the sporophytes in the preceding year that gives rise to sporophytes in the focal year. We added 10^{-3} to avoid the term being equal to zero for technical and biological reasons. Technically, the logarithm of $N_{y\text{-}1,p} = 0$ is not defined whereby $\log \mu_{y,p}$ and $N_{y,p}$ would not be defined. Biologically, $N_{y,p}$ may very well be > 0, although $N_{y\text{-}1,p} = 0$ as a result of immigration. The over-dispersion term $\varepsilon_{y,p}$ models excess variation compared to that assumed by the Poisson distribution (mean = variance). It also scales the abundance of the preceding year relative to all other sources of spores that may be the origin of the sporophytes in the focal plot and year. The term also includes effects of unknown local processes, e.g. intra- or inter-specific competition, or measurement error (residual variation).

Moreover, we modelled the logarithm of the regional, year-specific growth rate, $\log \lambda_y$, as a linear function of number of autumn frosts (F), spring precipitation (P) and spring temperature (T). Specifically,

$$\log \lambda_y \sim Normal(\mu_\lambda, \sigma_\lambda), \quad \text{eqn 3}$$

where σ_λ quantifies the inter-plot variation of $\log \lambda_y$, unknown regional processes, such as unexpected interaction effects between weather variables, or measurement error (residual variation), and where

$$\log \mu_\lambda = \varphi_0 + \varphi_1 \cdot F_y + \varphi_2 \cdot P_y + \varphi_3 \cdot T_y, \quad \text{eqn 4}$$

where φ_0 is an 'intercept' parameter and $\varphi_i \mid i = 1,2,3$ are 'effect-size' parameters. The parameters to be estimated were β_1, $\varepsilon_{y,p}$, φ_i, and σ_λ, and were assigned uninformative prior distributions.

The final model is the result of a selection procedure and model averaging based on the deviance information criterion (DIC), an information-theoretic criterion which is appropriate for Bayesian hierarchical modelling (Spiegelhalter *et al.*, 2002). In this case we needed to average two models as both were similarly adequate to explain the data variability. See further details in paper I.

Stochastic Growth Rates

We estimated the stochastic growth rate, $\log \lambda_S$, for the period 1996–2003, according to Lewonting & Cohen (1969):

$$\log\lambda_S \approx \log \bar{\lambda} - Var(\lambda_y)/2\,\bar{\lambda}^2, \qquad \text{eqn 5}$$

where $\bar{\lambda}$ is the geometric mean of λ_y (equation 4). This estimate accounts for the inter-annual variation in λ_y and for its full posterior distribution in every year, in any possible order of succession. We compared the posterior distribution of $\log \lambda_S$ with two of the most commonly used estimates of stochastic growth rate. The first was $\log \lambda_{SP}$, a point estimate of $\log \lambda_S$ as in equation 5, but only using the estimated modes of λ_y. The subscript *P* stands for 'point estimate'. The second estimate was derived from structured population models, and can be applied on any population time series (equation 14.59 in Caswell 2001; and references therein),

$$\log\lambda_{SL} = (1/T)\sum_{t=1}^{T}\log(N_{t+1}/N_t), \qquad \text{eqn 6}$$

where *t* are iteratively simulated years that tend to *T* –a large enough number of iterations for convergence to the expected value (Caswell, 2001), here *T* = 10000 iterations. N_t is the t^{th} element of a uniform random sequence of all the abundances simulated for the studied period. The estimate used was based on 100 independent estimates, each with a different random sequence of abundances. We henceforth refer to this estimator as the 'limit approximation', shortened $\log \lambda_{SL}$. Finally, we estimate approximate 95% confidence interval for λ_{SL} (Caswell, 2001),

$$\log\lambda_{SL}95\%\text{CI} \approx \log\lambda_{SL} \pm 1.96\sqrt{\frac{Var(\log(N_{t+1}/N_t))}{T}}. \qquad \text{eqn 7}$$

We inspect the effect of *T* on the estimate of the confidence interval.

3.1.3 Climate Change Scenarios

Using the final model described above, we conducted simulations of sporophyte abundance at the local (sample plot) scale for the period 1961 to 2098, driven by an ensemble of 13 climate projections (see below). Each climate projection provides yearly values of the climate variables (F_y, P_y and T_y; equation 4) that, together with the preceding years population size ($N_{y\text{-}1,p}$; equation 2) drive the population projection ($N_{1961\text{-}2098,p}$). Moreover, we accounted for regional and local scale variation and data uncertainty in the simulations by using the joint full posterior distribution of all model parameters.

Climate Datasets

We studied five sources of variation and uncertainty in climate (modelling; table 1) using an ensemble of regional climate change scenarios produced by the Rossby Centre regional atmospheric climate model RCA3.0 (Kjellström *et al.*, 2005; Samuelsson *et al.*, 2011). Emission scenarios included in the ensemble are the SRES A2 (comparatively high emissions) and B1 (optimistic low emissions) used to force ECHAM5. The main target of the ensemble is the uncertainty due to different driving coupled atmosphere-ocean GCMs under the SRES A1B scenario (Nakićenović & Swart, 2000; Randall *et al.*, 2007) that was greatly used in the recent-most IPCC fourth assessment (IPCC, 2007). We investigated the relative importance of four climate model-related uncertainty sources on population projections: 1) the GCM formulation, 2) the climate sensitivity, essentially the change in equilibrium global mean temperature resulting from a doubling of the greenhouse gas emissions, 3) the models' initial conditions resulting in variability at decadal and longer time-scales, and 5) the spatial resolution of the regional downscaling.

Simulation Summary

We summarized the simulated sporophyte abundance as the summed abundance among the six sample plots for three 40-years periods: 1961-2000 (reference period), 2019-2058 (near future) and 2059-2098 (far future). By having sampled the joint probability distribution of all parameters of the ecological model in the simulations, we obtained the probability distribution of the abundance for each year of simulation. The 50% and 90% highest posterior density intervals (HPDIs) for the posterior distributions of the abundance were calculated around the median.

We calculated the risk curves (probability of change in population abundance) for the two future 40-years periods, and for the different sources of

uncertainty in climate projections (table 1). Further details on how to calculate risk curves are described in paper II.

Table 1. *The ensemble of regional climate scenarios produced by the regional model RCA3.0 driven by different GCM scenarios and used for investigating effects of the emission scenarios and uncertainty sources on projected population abundance. RCM spatial resolution (RCM res) is 50 km if not otherwise stated.*

Region climate scenario characteristics		Emission scenarios and uncertainty sources				
Emission scenario	GCM driver	Emission scenarios	GCM formulation	Climate sensitivity	Initial conditions	RCM res. (km)
A2	ECHAM5-r1	Most severe				
A1B	ECHAM5-r1	Severe			X	
A1B	ECHAM5-r2				X	
A1B	ECHAM5-r3		X		X	50
A1B	ECHAM5-r3					25
A1B	ECHAM5-r3					12
A1B	CCSM3		X			
A1B	CNRM		X			
A1B	HadCM3-Q0		X	reference		
A1B	HadCM3-Q3			low		
A1B	HadCM3-Q16			high		
A1B	IPSL		X			
B1	ECHAM5-r1	Least severe				

3.2 Non-equilibrium Metapopulation Dynamics Model (III, IV)

3.2.1 The Epiphytic Lichens Study System

The study area (1750 km^2) covers the forest landscape of Halmstad Municipality, County of Halland, southern Sweden (56º 46' N 13º 4' E) (figure 4a). It is situated in the transition zone between the nemoral and hemiboreal regions (Jonsell, 2004). Less than 8% of the European beech (*Fagus sylvatica*) forest area present in the mid-1600s remains, as estimated from historical maps. As much as 4.8% of the study landscape is currently protected (10% of the beech forest within the study landscape; figure 4b). According to the plans of Halland's county administration, these figures will rise to 6.3% (21% of the beech forest). These figures are high compared to the average of 1.5% productive forest that is currently protected in Sweden (Forestry Board, Unpublished data). There an area defined as "high conservation-value for broadleaved forest" with high priority for conservation (Forestry Board, Unpublished data), which covers 84% of beech forest in the study landscape.

Beech-dominated stands (focal stands, henceforth) were selected from an inventory of broadleaved stands (Forestry Board, Unpublished Data), using the following criteria: (1) stand area ≥0.5 ha and ≤5 ha, and (2) average estimated age ≥95 years. In selected stands, beech dominated with an average of 80% of standing volume, followed by oak (*Quercus robur*) and other broadleaved trees (each <10%), and Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies;* each <5%). We recorded the age of focal stands by coring the four trees that were considered to be the oldest trees in the stand. The mean stand age was 160 (±40) years. For further details on the age estimate see paper III.

Focal stands were surveyed in 1998 for presence-absence data on nine epiphytic crustose lichens (table 2) that are confined to beech in the study region (Ö. Fritz, pers. com.). This host-tree specificity made us assume that beech stands are patches for the epiphyte metapopulation. The study species are red-listed in Sweden (Gärdenfors, 2010), or indicator species of a high probability of occurrence of red-listed species (Nitare, 2000).

We assume that the minimum stand age at which an epiphyte species was recorded is a species-specific lower limit of one dimension of their realized niche (Devictor *et al.*, 2010), the minimum suitable age henceforth (table 2). The minimum suitable age will determine the species-specific number of suitable stands (habitat patches) in the landscape. We only included in the study stands that became suitable for colonization after 1850, because it was not possible to estimate potential sources of colonization before this point in time. Included stands also were at least as old as the minimum suitable age in 1998. See table 2 for the final number of focal stands per species.

Table 2. *Epiphytic lichen species included in the study. We show the minimum suitable age, Red List category (VU= vulnerable, NT= near threatened or EN= endangered; Gärdenfors 2010), or whether the species is an indicator species (Ind; Nitare, 2000), the occupancy in 1998, and the number of focal stands (N) used for model fitting.*

Species	Minimum suitable age	Red List category	Occupancy (%)	N	Dispersal limited	Paper
Bacidina phacodes	118	NT	9	90	No	III
Chaenotheca brachypoda	118	Ind	12	91	Yes	III, IV
Lecanora glabrata	86	NT	35	99	Yes	III, IV
Megalaria laureri	120	EN	9	90	No	III
Opegrapha viridis	113	Ind	11	97	Yes	III, IV
Pachyphiale carneola	120	VU	11	90	Yes	III, IV
Pertusaria multipuncta	120	VU	25	90	No	III
Pyrenula nitida	86	NT	43	99	Yes	III, IV
Thelopsis rubella	120	VU	4	90	No	III

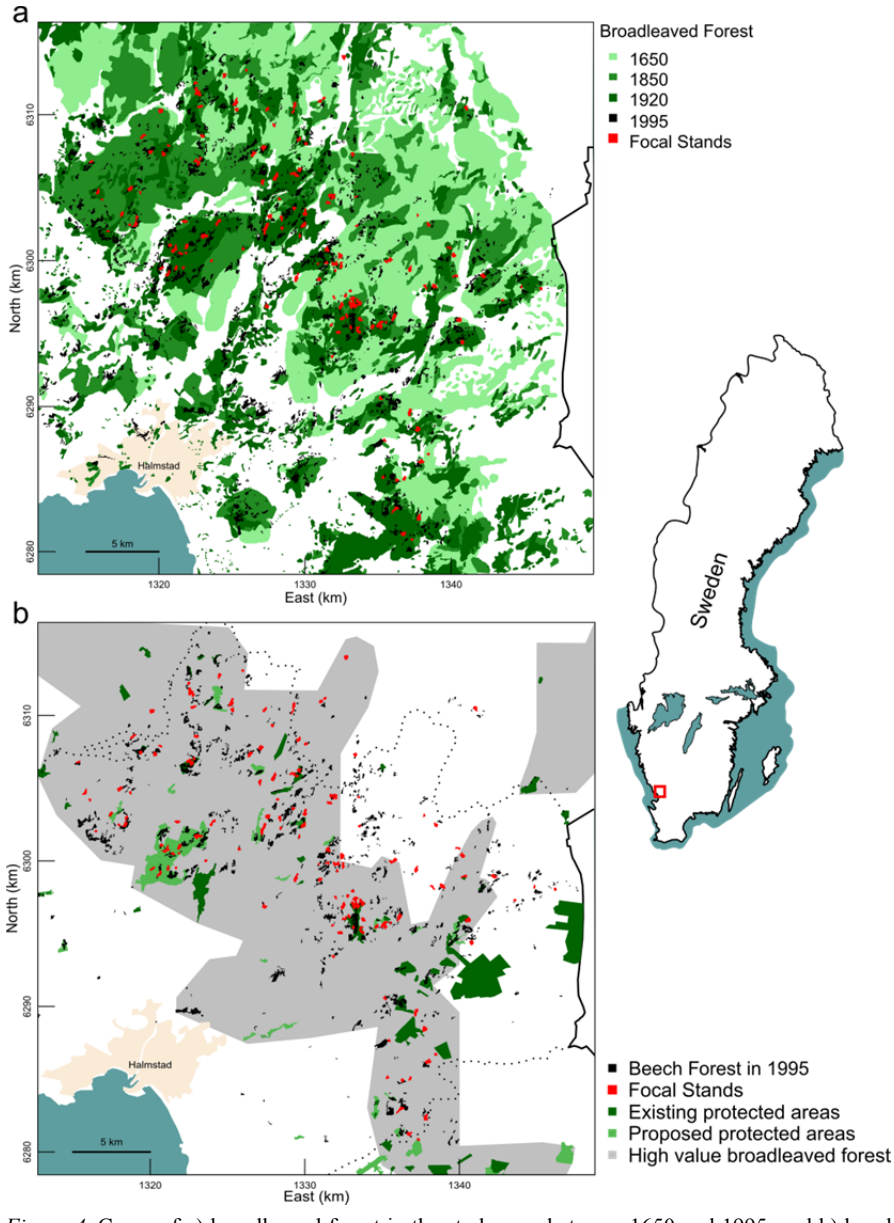


Figure 4. Cover of a) broadleaved forest in the study area between 1650 and 1995, and b) beech forest in the study area in 1995 (Forestry Board, Unpublished Data). The surveyed beech stands are shown in red. The black line shows the limits of the county of Halland. Halmstad city is lightly shaded.

3.2.2 The Model

To estimate the colonization rates of each species we developed a model that allowed us to estimate time- and patch-specific probabilities of species occurrence in the beech stands, i.e. to estimate the time series in species occurrence for each stand. We assumed that the occupancy pattern of the species, i.e. the distribution of the species among forest stands observed in 1998 was the result of colonization events that took place after the focal stands became suitable, and that the species is thereafter dispersed within each stand. More specifically, we modelled the species occurrence ($F_{i,t}$) in each focal stand i every ten-year time steps t, between the species-specific minimum suitable age (figure 5) and 1998. The response variable $F_{i,t}$ take the values 1 – species present, 0 – species absent, or NA – missing observation. If $F_{i,t}$ = NA, the presence is estimated based on the non-missing observations and the estimate of the remaining parameters (Gelman *et al.*, 2004). We assume that the number of propagules arriving to a focal stand follows a Poisson distribution, so that the probability of at least one successful colonization is $\eta_{i,t} \sim 1\text{-}e^{-\varphi}$, where φ is the mean colonization rate. We further assume that

$$F_{i,t} \sim \text{Bernoulli}(\eta_{i,t}), \qquad \text{eqn 8}$$

where the Bernoulli distribution has a mean $\eta_{i,t}$, and this mean depends on the occurrence of the species on stand i at time t-1 as

$$\eta_{i,t} = \zeta_{i,t}^{\tau_{i,t}};\ \tau_{i,t} = \begin{cases} 1, F_{i,t-1} = 0 \\ 0, F_{i,t-1} = 1 \end{cases}. \qquad \text{eqn 9}$$

As a first approach, we assumed no stochastic extinctions from occupied stands, i.e. once a stand becomes colonized it can only remain occupied (if $F_{i,t-1}$ = 1, then $\eta_{i,t} = \zeta_{i,t}^{0} = 1$; else $F_{i,t-1} = 0$, then $\eta_{i,t} = \zeta_{i,t}$, figure 5). The parameter $\zeta_{i,t}$ is the realized colonization rate –i.e. a time-step and patch specific colonization probability–, and was further modelled as

$$\text{cloglog}\left(\zeta_{i,t}\right) = \log(\varphi) + \log(T_i) + \log(S_{i,t}), \qquad \text{eqn 10}$$

where φ is the mean colonization rate, T_i, is a time-independent measure of stand suitability, and $S_{i,t}$ is a measure of connectivity. The stand suitability measure T_i is described as $\log(T_i) = \beta \boldsymbol{X}$, where β is a vector of associated effect size parameters, and $\boldsymbol{X}$ is a matrix of local environmental covariates that are not subject to change over time. We included as environmental covariates the stand's aspect (degrees from south in absolute value), slope (%), productivity index of beech forest (m^3 of forest · ha^{-1} · $year^{-1}$), and a proxy of forest continuity used by Fritz *et al*. (2008) to analyse this data set.

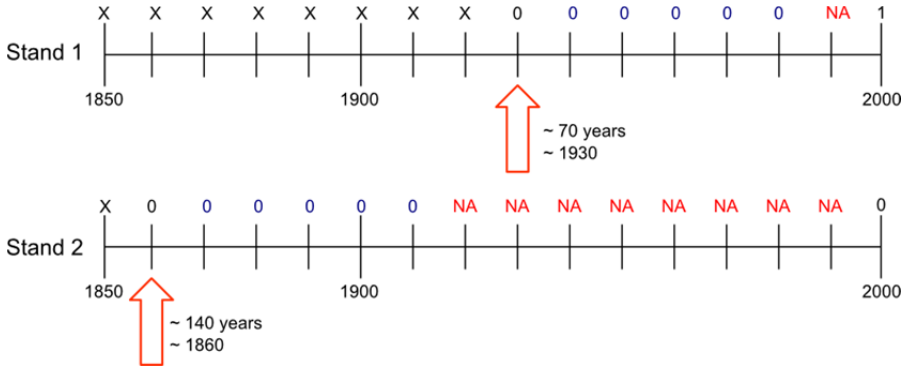


Figure 5. Schematic description of the modeling approach. X represent years when the stand was not present, 1 means species present, 0 means species absent, blue 0 means species absent because the minimum suitable age has not been reached (assuming a minimum suitable age of 50 years), and NA means missing observation to be estimated.

Since the landscape changed drastically during the last 150 years, we assumed that connectivity, $S_{i,t}$, is best represented by the amount of forest available (and potentially occupied) around a focal stand at time t. We estimated connectivity for three periods based on the broadleaved forest present in 1850, 1920 and 1995 shown on historical maps (figure 4a). We divided the historical maps into a 300 by 300 m grid, and measured the distance ($D_{i,j}$) from the centroid of the focal stand i to the centroid of the grid square j were there was broadleaved forest within a radius of 10 km from the focal stand i. The connectivity measure $S_{i,t}$ follows a negative exponential distribution. This relationship assumes independent colonization success among propagules, which is biologically reasonable for our study species.

We assume that once a species has colonized a focal stand, it does not go extinct from it. The extinction rate from trees that remain standing has been shown to be negligible for many cryptogamic epiphytes (Snäll *et al.*, 2003; Johansson *et al.*, 2012; III; but see Öckinger & Nilsson, 2010; Gjerde *et al.*, *in press*). Hence, we also assume that the last occupied tree in the stand will never fall. We test the sensitivity of these assumptions by also fitting a model with unknown, but low, stochastic extinction rates (III).

Each final species-specific model is the result of a selection procedure based on the mean of the deviance posterior distribution, which is a Bayesian measure of model fit or 'adequacy' (Spiegelhalter *et al.*, 2002). See paper III for further explanations on selections criteria. We first compared the null model with the spatially explicit model, to later build upon the best resulting model, including the environmental covariates.

For species where $S_{i,t}$ was included, i.e. spatially explicit models, we estimated the median dispersal distance as an approximation (underestimation)

of the species dispersal kernel –i.e. a measure of the effect of the surrounding patches on the colonization probability of a focal patch. We defined the median dispersal distance as the distance where up to 50% of the colonization events are likely to occur.

To investigate the behaviour of the spatially explicit models we run simulations for 100 years with both null and spatially explicit models, using the landscape configuration observed in 1998. We expect lower projected occupancies by the spatially explicit models than by the null models. We also compared our results with estimated confidence limits of the expected occupancy given that the equilibrium assumption holds. The occupancy at time t (O^*_t) assuming equilibrium was defined as $O^*_t = \sum_i^{n_t} F^*_{i,t}/n_t$, and $F^*_{i,t} \sim Bernoulli(O_{obs})$, where $F^*_{i,t}$ is the species occurrence at focal patch i in time-step t assuming equilibrium, O_{obs} is the occupancy observed in 1998, and n_t is the number of patches in time t which remained constant during the projection.

3.2.3 Forest Management Scenarios

Simulations were performed for dispersal limited species (table 2), based on the spatially explicit non-equilibrium metapopulation models previously fitted. The simulations were based on the configuration and occupancy of the beech-dominated forest stands observed in 1998 (Forestry Board, Unpublished Data). Each beech stand in the study landscape with an age equal to or larger than the species-specific minimum suitable age (table 2) is assumed to be a potential dispersal source for the epiphyte species. The focal stands of paper III were set as "observation units", and were not subject to any management. Simulations were run for 150 years –ten years longer than a typically high rotation time for commercial beech forest in the region. The following scenarios of protection of the remaining beech forest were set:

- Preserve 0% of beech forest in the landscape,
- Preserve 1.5% of beech forest, i.e. mean national level of protection of productive forest,
- Preserve 10% of beech forest, i.e. the existing set up of protected areas in the county of Halland,
- Preserve 21% of beech forest, i.e. the existing and proposed set up of protected areas in the county of Halland. The protection level in this scenario is above the 17% target agreed in the Aichi Biodiversity Targets (Convention on Biological Diversity, 2010),
- Preserve 84% of beech forest, i.e. all beech forest included in the "high conservation-value area for broadleaved forest" (Forestry Board), and

- Preserve 100% of beech forest in the landscape. This scenario is a theoretical maximum reference level.

Non-protected forest stands were cut under a "business as usual" scenario, i.e. 8.3% of total beech forest area per decade, which equals approximately one stand every 120 years. According to current forestry practice in the county, when a stand is cut, 40% of the standing volume including the oldest trees is retained for at least ten years. In the next 30 years the remaining trees are cut progressively until the retention level is met. The retention level is the proportion of the stand area to be retained for conservation after cutting. To explore the effect of different management strategies of productive forest on the epiphyte metapopulation viability, we determined three levels of productive forest retention:

- 0%, i.e. no retention actions,
- 5%, i.e. the common practice, and currently minimum recommended in the county (Bernt Flink[2] pers. com.),
- 15%, i.e. a high but realistic retention level.

We assumed that the stands' potential as source of dispersal is linearly related to the retention level. Later, when the time since the first cut is equal to the minimum suitable age plus an assumed epiphyte generation time of 20 years (Lättman *et al.*, 2009; Gärdenfors, 2010), the stand is assumed to have recovered as a source of dispersal.

We obtained the posterior probability distribution (PPD) of the simulated occupancy. To measure the relative effect of different beech-forest protection and retention level scenarios on the species occupancy, we calculated the probability for the occupancy PPD under any scenario being greater than the scenario where nothing is protected nor retained. Probabilities were calculated as $\frac{\mathrm{P}(Scn>R)}{0.5} - 1$, where *Scn* is the occupancy PPD under a focal scenario, and *R* is the occupancy PPD under reference scenario. We draw 10000 samples from each PPD to ensure convergence to a point estimate of the probability.

[2]. Forestry Board in Halland.

4 Results and Discussion

Our results depict a negative situation for the studied species. *Buxbaumia viridis* is predicted to decline in the study area both under current conditions (I) and under future climate scenarios (II). The metapopulation dynamics of epiphytic lichen species on beech are best estimated by non-equilibrium metapopulation models, given the severe history of habitat loss and fragmentation in the region (III). Protected areas alone may not improve metapopulations viability, and may need to be aided with strong complementary conservation strategies (IV).

4.1 Hierarchical Population Dynamics Model

The hierarchical Bayesian approach adds a fundamental aspect to the population viability estimate: natural variability and sampling uncertainty across regional and local scales (Clark & Bjørnstad, 2004) for species living in temporally and spatially varying environments. This approach allows the stochastic growth rate to be estimated under all possible combinations of the observed environmental variability. Therefore, we can provide an estimate of confidence in the statement about the long-term viability of the population. The approach also allows disentangling the relative importance of different drivers of the inter-annual variation in population abundance.

Our model suggests that the population of *Buxbaumia viridis* at the study site will decline in the long term under environmental conditions that are similar to current conditions; i.e. the mode for the stochastic growth rate, a widely used measure of population growth in fluctuating environments (Caswell, 2001), was <0 for all three estimators of log λ_S. However, previous estimates of the stochastic growth rate did not account for uncertainties in a coherent and satisfying way. First, point estimates (single values) such as log λ_{SP} or log λ_{SL} cannot, by definition, express any variation. Second, the estimate

of the confidence interval based on the limit approximation approach (Caswell, 2001) underestimates uncertainties. The main reason for the latter is that the approach aims to estimate the mean of the growth rate, with the confidence interval representing the uncertainty in the estimate of this mean. That is, the confidence interval does not reflect the natural variation and uncertainty in the population growth rate, which is however, accounted for in the hierarchical model. It should also be noted that the width of the interval decreases the longer the analyst runs the projections, i.e. how large T is chosen to be in equation 7. Furthermore, the estimate of the confidence interval of log λ_{SL} using the limit approximation approach suggested no population decline since the interval included zero. This categorical conclusion could have negative consequences if used in conservation strategies.

In contrast, the full probability distribution of the estimate of log λ_S provides information on how likely a population decline is, or the confidence in a statement about a decline. We can state that the probability of decline is 81%, which is more informative and can be weighed against other interests. The full posterior distribution of log λ_S presented in the current study explicitly utilizes the full posterior distributions of the year-specific growth rates (i.e. their natural variability and uncertainty), and thereby accounts for all possible combinations of year-specific population growth rates and their relative effects. Equation 5 includes the geometric mean (first term), which give high weight to values (of λ_y) close to zero, and it includes the variation in yearly growth rate (second term).

Lewontin & Cohen (1969), who presented this estimator, compared the problem of viability of small populations with the problem of growth of a repeatedly gambled capital. Let us consider the following example. Assuming that the odds of winning in a casino is "slightly" against us –e.g. the probability that we lose a gambled chip in a specific game event is 55%[3]–, we convert our capital into a population of "casino chips", and we put them a Latin name of preference. We visit the casino repeatedly during, let us say, two weeks. Even if we have won in 45% of the times, there are two possible outcomes. Either, we become active conservationist of our Latin-named population of chips. We could even set aside parts of the population from the gambling threats. Or we become gamblers.

Species Population Dynamics and Life Cycle

According to the final averaged model, the regional-scale weather variables had larger effects than the local-scale abundance in the preceding year on the

[3]. In the frequentist approach we might even say "well, the odds are not really different from a 50-50 chance".

abundance of sporophytes in a focal year –the standardized effect-size parameters for frosts, precipitation and temperature were larger than the effect-size parameter for abundance in the preceding year (figure 6). The population dynamics are mainly driven by regional weather fluctuations, which have also been shown to have a key influence on the demographic processes of some vascular plants (e.g. Ågren *et al.*, 2008; Evju *et al.*, 2010; Jongejans *et al.*, 2010; Toräng *et al.*, 2010). The first likely regional environmental mechanism driving the population dynamics is sudden spells of freezing before the winter, causing high mortality among immature sporophytes, as observed for the congeneric *B. aphylla* (Hancock & Brassard, 1974). The second is water stress resulting from high temperature and low-precipitation conditions, which decreases survival of the sporophytes in the spring (Wiklund & Rydin, 2004). The local-scale variable abundance in the preceding year had a small, yet positive, effect on the abundance in the focal year, and we decided to keep it because it makes sense biologically. The small effect of this variable support the hypothesis that *B. viridis*' spore germination and fertilization can occur within one year after the spore release. We also think that there may be a considerable spore rain from outside the study plots, and that, hence, the preceding year's abundance in a sampling plot is not the only spore source.

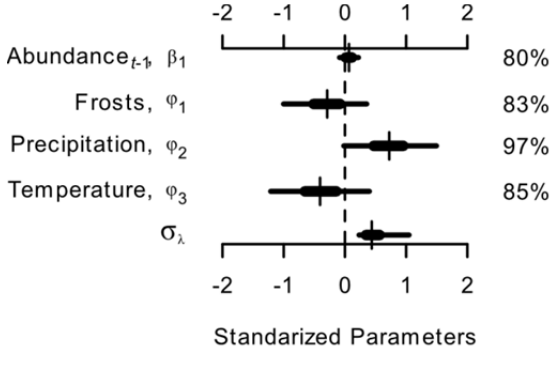


Figure 6. Parameter estimates for the final model for the population dynamics of *Buxbaumia viridis*. The parameters are associated with the abundance in the preceding year, autumn frosts, spring precipitation and spring temperature. The modes (short vertical lines), 50% (thick horizontal lines) and 95% (thin horizontal lines) highest posterior density intervals are shown. To the right are the proportions of the posterior distributions being higher or lower than 0. The dashed (0) vertical line is a visual aid.

Uncertainty was well captured as we modelled unknown processes at the regional as well as at the local scale. The parameter σ_λ quantifies the inter-plot variation in population growth rate. In addition, the parameter $\varepsilon_{y,p}$ scaled the local recruitment from sporophytes in the preceding year accounting for unknown local recruitment processes, e.g. germination of spores from the spore bank, or measurement error.

We now know that the persistence of this species is determined by a combination of regional processes (weather variability), and local population dynamics (preceding year's abundance). A change in the variability or in the balance between these processes may lead to a further decline of the species. Short-lived species, such as *B. viridis*, may be more sensitive to increments in environmental variability than long-lived species (Morris *et al.*, 2008).

4.1.1 Climate Change Scenarios

Our results show that the strength in statements about population changes in the future may vary significantly depending on the number of uncertainty sources that are accounted for in the projections. We should be aware of this for providing robust pictures for evaluating risks. Population viability analyses acknowledging the uncertainty in climate change are increasing, but the influence of different uncertainty sources on the statements about the population development has, to our knowledge, never been disentangled. Increased understanding of the relative importance of different uncertainty sources also helps choosing which sources to include when conducting studies on the impact of climate change. This additional information helps to prioritize among competing demands.

The future decline of the *B. viridis* abundance is observed under the three IPCC SRES scenarios forcing ECHAM5 (figure 7). We have expressed the uncertainty in the form of risk curves (probabilities of change in population abundance). The decline in population abundance is illustrated by an increase in probability of population decline to low levels (figure 7). There is a more than 65% risk for the population to be halved (i.e. decline by 50% or more) in the far future under SRES B1 scenario. These probabilities of decline to different levels are straightforward to apply in conservation planning and decision making.

Three out of four of the studied sources of uncertainty related to climate modelling contribute to the uncertainty in the projected levels of *B. viridis* abundance. The greatest source of uncertainty is GCM formulation. The variation in the probability of population decline in the near future among different SRES scenarios is smaller than the variation among simulations of the A1B scenario driven by different GCMs formulations (figure 7b). However, this difference in variation among emission scenarios and GCM formulation tends to disappear in the far future: there is similar variation among GCM formulations as among emission scenarios. The GCM parameterization (i.e. climate sensitivity) had influence on the population projections (figure 7c). The model with the reference level in climate sensitivity (HadCM3-Q0) presented

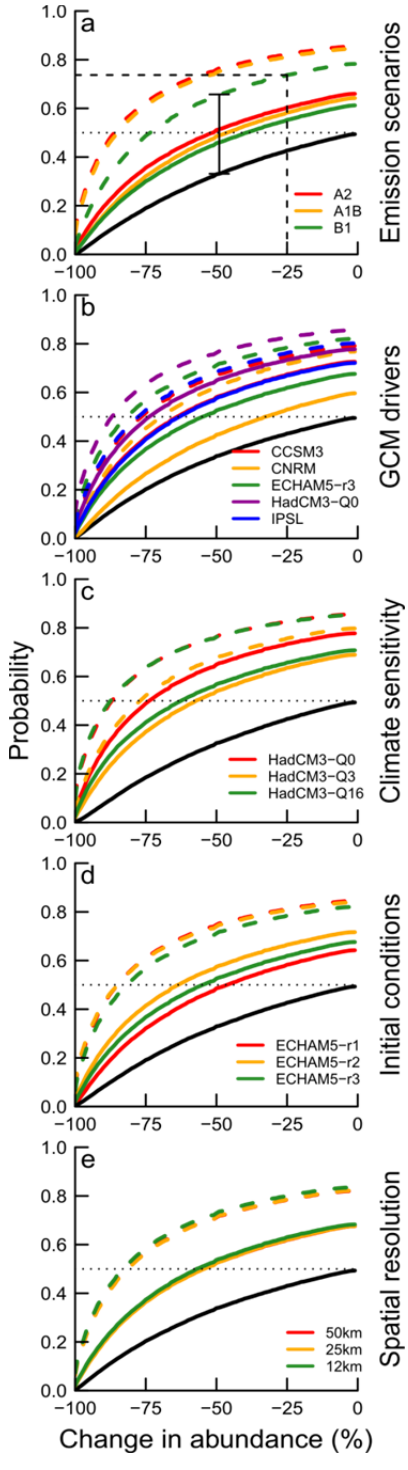


Figure 7. Risk curves for *Buxbaumia viridis*. The percentage of decline are in relation to the reference period 1961-2000, assuming different emission scenarios (a), different GCM drivers (b), climate sensitivity (c), initial conditions (d), and spatial resolution (e). Each point on the curves shows the probability that the population abundance will decline in relation to the reference period by at least the given percent during 2019-2058 (solid lines) and 2059-2098 (dashed lines). The black line represents the reference period (1961-2000) for every model. The dashed lines (a) illustrate the principle for reading the probability of decline to a certain level, here a 73% risk for a 25% decline *or more*. Probabilities are cumulative towards zero. The whisker (a) illustrates the largest difference between the probability distribution of abundance change and the reference probability distribution, i.e. the most likely event. The horizontal dotted line is a visual aid at 50% probability.

the highest increase in probability of decline in the near future. The natural variability in the slow components of the climate system, variability in initial conditions of the oceans phase, is also an important source of uncertainty (figure 7d). However, its importance decreases the longer the simulations are run, in accordance with pure climate simulations (Kjellström *et al.*, 2011). As expected for variables that do not represent extreme weather events, the spatial resolution of the RCM had a negligible influence on the variation in probability of bryophyte population decline (figure 7e). The spatial resolution is not important when using climate data that have been aggregated over longer time periods, as we do (Nikulin *et al.*, 2011).

4.1.2 Model Restrictions

We are aware of the risk of underestimating the environmental variability when using time series data (Beissinger & McCullough, 2002), as the approach was fitted only to observed environmental variability. However, the weather data represent the conditions of the last decades of the century (paper I). Moreover, since both the autumn and spring weather have changed during the last century in the study region (IPCC 2007), statements about population viability based on environmental conditions observed long ago, when they were different, would be inaccurate. We therefore think that our estimate of population viability is reliable, as long as the weather conditions remain approximately the same.

A limitation of the performed simulations is that the ensemble uses a single GCM to compare scenarios. However, the relatively large variability introduced by different GCM in near future agrees with earlier population projections and analyses of variation among climate models (Snäll *et al.*, 2009; Kjellström *et al.*, 2011). It is known that the RCM used in this ensemble (RCA3.0) is biased by overestimating the summer precipitation in northeastern Europe (Kjellström *et al.*, 2011). This means that the viability of this and similar species may be even worse.

Table 3. *Difference in deviances from the null model for metapopulation models for the lichen species. Final models are indicated in bold font. From the first to the fourth model (2nd to 5th column) the terms were included stepwise, starting with the null model which only includes a mean colonization rate. Parameters in fifth to tenth model were independently tested based on the best fitting model from the left section. ":" indicates interaction. Ext means Extinction. Prod means Forest Productivity index.*

Species	Null Model	Spatial Model	Ext	Slope	Aspect South	Slope · Aspect	Area	Prod	Forest continuity
B. phacodes	**0**	-2.2	11.8	-0.2	-0.5	0.4	0.1	-0.2	0.2
C. brachypoda	0	**-3.6**	13.1	0.7	-0.1	1.3	0.3	-0.6	-0.4
L. glabrata	0	**-6.7**	77.4	-0.9	0.1	-1.2	0.0	0.1	0.5
M. laurei	**0**	-1.8	8.3	0.0	-0.7	-0.1	0.7	-0.9	-0.3
O. viridis	0	**-4.4**	6.7	1.6	-1.7	-4.9	-1.8	-0.8	0.0
P. carneola	0	**-3.2**	11.8	0.9	0.5	-0.4	0.3	0.0	-0.5
P. multipuncta	**0**	-0.6	10.4	-0.1	0.1	-0.5	0.1	0.0	0.0
P. nitida	0	**-7.1**	86.9	0.4	0.5	-1.4	-1.1	-0.1	0.5
T. rubella	**0**	-1.0	7.0	0.1	0.0	0.8	-0.2	-0.7	-0.6

4.2 Non-equilibrium Metapopulation Dynamics Model

We present an approach to estimate colonization and extinction rates of non-equilibrium metapopulations based on data on their occurrence pattern in the landscape and on the historic distribution of their patches. By estimating the colonization events leading to the observed pattern of occupied and non-occupied patches, we have estimated the mean and realized decade-specific colonization rates of the study species. For five out of nine species (*Chaenotheca brachypoda*, *Lecanora glabrata*, *Opegraha viridis*, *Pachyphiale carneola* and *Pyrenula nitida*) the colonization models were improved by adding the connectivity measure (table 3). We show that for dispersal-limited species in a severely fragmented landscape, we may overestimate the colonization rate of sessile species if we do not take into account the landscape history.

When the landscape has undergone severe habitat loss or change in a relatively short time –from the perspective of a species– equilibrium is an assumption that cannot be made (Hanski *et al.*, 1996; Moilanen, 2000). Under equilibrium one would expect that the occupancy pattern of the metapopulation reflects the spatial structure of the landscape (Hanski, 1999). The model presented accounts for the creation of the patches and for the past spatial structure of the landscape so neither the past, nor the future occupancy is assumed to be within the limits set by an equilibrium assumption (figure 8). The estimated past time series and the projected future time series on occupancy, i.e. before and after 1998, respectively, are different from occupancies estimated by the equilibrium models (right panel, figure 8).

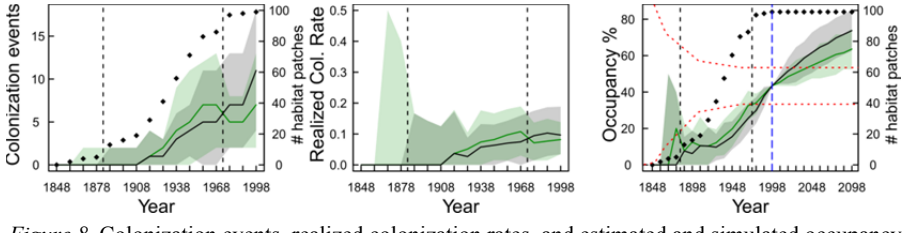


Figure 8. Colonization events, realized colonization rates, and estimated and simulated occupancy over time (before and after 1998, respectively) for *Pyrenula nitida*, as an example. The median (solid lines) and 95% (shades) highest posterior density intervals (HPDI) are shown. Dots in the left and right columns show the number of suitable forest stands. Black dashed lines show the change in landscape. Blue dashed lines show the observation year. Red dotted lines show the 95% HPDI of the expected occupancy under the equilibrium assumption.

Increasing fragmentation slowed down colonization of five study species that are dispersal-limited, thus null models overestimate its realized colonization rates. Colonization events in a null model are only constrained by time

dependant density of patches. Based on the reconstructed time series on patch specific species occurrence we could calculate the number of colonization events every time step (left panel, figure 8), and the realized colonization rate based on unoccupied patches (center panel, figure 8). However, colonization events in a spatially explicit model are constrained by time dependant density of patches and by the configuration of the surrounding landscape. Therefore, in a spatially explicit model realized colonization rates decrease with increased fragmentation, i.e. mainly after 1978 (figure 8).

The choice of modelling approach has important implications when applying the models for metapopulation viability analysis. We show how different assumptions lead to very different projections of future metapopulation dynamics, i.e. equilibrium versus non-equilibrium models or spatial versus non-spatial models. The difference between the models becomes clear in projections of future metapopulation dynamics. Even for a species like *O. viridis*, where the difference between the models is barely evident based on model deviance (table 3), the projected occupancies are lower with the spatially explicit model than with the null model.

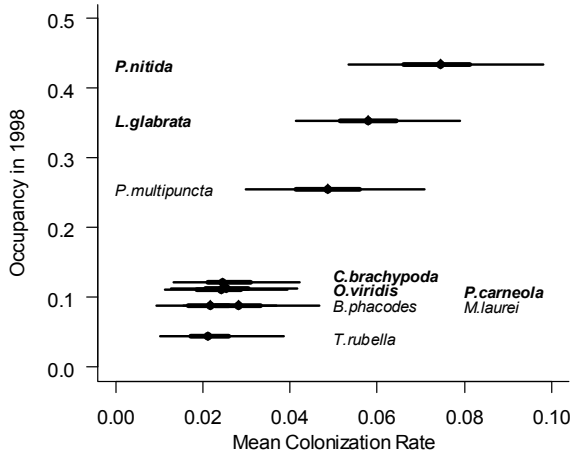


Figure 9. Mean colonization rates (φ) per decade, versus observed occupancy. Modes (dot), and 50% (thick horizontal lines) and 95% (thin horizontal lines) highest posterior density intervals of colonization rates are shown. Species for which the dynamics are better explained by spatially explicit models are indicated with bold font.

Our models suggest that colonization rates cannot always be inferred from the proportion of occupied patches in the landscape, the occupancy. Different occupancies can be reached with similar mean colonization rates. Especially in rare species, as red-listed species often are, the relationships were weak (figure 9). For more frequent species, the occupancy and colonization rate are positively correlated (O_{obs} >21%). The density of patches in the landscape is determined by the species-specific minimum suitable age, the lower limit of one niche dimension. Therefore, species with the highest minimum-suitable age perceive a lower amount of patches to colonize, and have the lowest

occupancies (figure 9). Interestingly, among the species with low colonization rates, the ones that seemingly disperse short distance have higher occupancies. This suggests that dispersal-limited species have higher establishment rates (Löbel & Rydin, 2009) or larger diaspore outputs. *Pertusaria multipuncta* is the exception as it has a relatively high colonization rate and occupancy on a low density of patches as defined by high minimum suitable age.

Our models suggest that stand-level stochastic extinctions are negligible, whereby the extinction rate is deterministically set by the rate of patch destruction (patch-tracking metapopulation dynamics; Snäll *et al.*, 2003). These dynamics have been supported at the stand-scale in some, but not all vascular plants (Verheyen *et al.*, 2004; Jäkäläniemi *et al.*, 2005). At the tree scale, it has been supported in crustose lichens (Gjerde *et al.*, *in press*; Johansson *et al.*, 2012) and epiphytic bryophytes (Snäll *et al.*, 2003). However, it has been rejected for foliose-lichens (Öckinger & Nilsson, 2010; Fedrowitz *et al.*, 2012), and for an epiphyllous bryophyte (Zartman *et al.*, *in press*). Although the current models do not include an estimate of stochastic extinction rates, it does implicitly account for deterministic extinctions driven by habitat loss and fragmentation. In an unmanaged forest where the age structure is determined by gap-dynamics, as in beech forest (Peters, 1997), a relatively low stochastic extinction rate at the tree scale should result in a lower or even negligible stochastic extinction rate at the forest stand scale.

The effect of surrounding forest (the estimated dispersal kernels) seems to depend on the spatial scale the study is focused on. Other studies for epiphytes report mean dispersal distances of 16 to 50 m (Snäll *et al.*, 2003; Öckinger *et al.*, 2005; Werth *et al.*, 2006; Johansson *et al.*, 2012), when focusing on individual establishments within ranges of 24 to 210 ha. In the present study, we focus on the dispersal between forest stands within an area of 175 000 ha, and we found median dispersal distances between 120 and 2650 m. Even for *O. viridis*, that presented the shortest median dispersal distance, more than 10% of the spores arriving to a focal stands could have come from distances longer than 500 meters. The longer dispersal distances we found at a large scale may explain what, at a smaller scale, Johansson *et al.* (2012) described as background deposition. A background deposition at a much larger scale (Muñoz *et al.*, 2004), may in turn explain the lack of dispersal limitation within this landscape found for some of the species here modelled.

Many environmental variables used to explain distribution patterns mix the relative importance of habitat quality or quantity with the effect of time itself as exposure to propagules (Nordén & Appelqvist, 2001). While local time-dependent environmental variables (e.g. forest continuity, tree diameter, tree age) may explain distribution patterns (Snäll *et al.*, 2004; Fritz *et al.*, 2008,

2009), non-equilibrium approaches, such as the one here presented or Snäll *et al.* (2005), found no support for the effect such variables on the colonization rates of the same species. This means that the duality of the time-dependent environmental variables may have been disentangled with non-equilibrium dynamic models. However, although our data does not support an effect of local time-independent environmental variables on the colonization rates, there is evidence to support that stand productivity index may affect habitat suitability and, therefore the colonization rates (Fritz *et al.*, 2008).

4.2.1 Forest Management Scenarios

A protection target even higher than the one set by the Convention on Biological Diversity (CBD; 2010) does not improve the viability of the study species in an already highly fragmented landscape. We show that future occupancies of epiphyte metapopulations in stands that are suitable for colonization may not be different in landscapes where up to 21% of the remnant beech forest is protected than occupancies in landscapes where nothing is protected (figure 10). Only under unrealistic forest protection scenarios (84 and 100% of remnant beech forest protected) there is substantial support for increment in epiphyte occupancies (figure 10). However, higher retention levels are likely to improve the landscape connectivity.

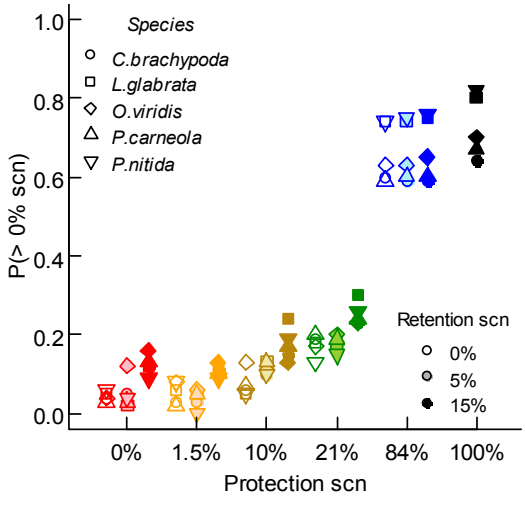


Figure 10. Probabilities of improvement in viability (simulated occupancies being higher than occupancies under a scenario of no protection nor retention) after 150 years of simulation. Scn means scenario. Different colours are a visual aid to identify protection scenarios

During simulations, occupancies increased under every scenario. Increased occupancy on sampled stands is not necessarily a sign for viable metapopulations. This result indicates that sample stands are still under initial colonization process, and some of stands are well enough connected to be colonized before the next 150 years. The occupancies reached during

simulations would probably level out as the metapopulation reaches equilibrium with the simulated landscape configuration. Thus, occupancies at equilibrium will mainly depend on the patch extinction rate (Hanski *et al.*, 1996), in this case determined by forest management. As with local populations, the larger the metapopulation size the higher the metapopulation viability and the lower the impact of catastrophes and environmental variability (Hanski & Ovaskainen, 2000; Ovaskainen, 2002). Given the severe fragmentation that the landscape has undergone, and the lack of information about the viability of epiphyte metapopulations, we assume that is a good conservation practice to evaluate forest management measures to preventively increase the metapopulations viability.

Protected areas can be effective refuges for sessile species on their own, but it is not likely that they will improve metapopulation viability. The study landscape is an example of a relatively well protected landscape, where 10% of the remaining beech-forest is under protection, and 11% more is to be protected in the near future. Protecting up to 21% of the forest would certainly add effective refuges against habitat loss. However, in severely fragmented landscapes, these levels of forest protection may not be able to sustain metapopulation dynamics if connectivity is not otherwise improved. It is thus a matter of time for the occupancy to decrease due to extinction debt (Tilman *et al.*, 1994).

Forest retention actions can help to improve the landscape connectivity. Improved viability obtained with simulated retention actions is promising. Higher retention levels increase the chances for long-term persistence of the metapopulation. However, further investigations are needed on the actual value of forest retentions as dispersal sources, as well as on the effect of the spatial configurations of retained trees –i.e. retained patches vs. dispersed retained trees.

4.2.2 Model Restrictions

Our simulations have limitations that are important to acknowledge. First, it is important to bear in mind that the simulations are run based on sample stands that are not subject to forestry activities in simulations. Therefore, we cannot estimate the extinction risk. We estimate the increase in occupancy under different scenarios of landscape configuration, as a measure of improvement on metapopulation viability (Ovaskainen, 2002). Second, there are some assumptions in the model derived from available data, for which we could not account for its uncertainty in the simulations. For example, by using all forest stands with the potential of being sources of dispersal, as a proxy for the actual sources of dispersal we may overestimate the connectivity between patches.

Therefore, occupancies may be even lower than projected. Also, the stands' minimum suitable age may not be deterministic, and may be dependent on local environmental variables (Fritz *et al.*, 2008). Estimating and incorporating this uncertainty would make the "creation" of patches (i.e. the moment when the species start perceiving forest stands as suitable habitat) a stochastic process. Overestimating the minimum suitable age, by underestimating the presence of the species in younger stands, may lead to less habitat patches in the landscape, thus overestimating the colonization rate. Very little is known about the generation time for epiphytic lichens. Therefore we had to use estimations from a few studies, not including our study species. The generation time may be species-specific, and depend on local environmental conditions (Lättman *et al.*, 2009; Høistad & Gjerde, 2011), and may influence the assumed time until potential sources of dispersal recover their full potentiality. However, given that we only simulate one rotation period, results are not very sensitive to this assumption. It may be important for longer simulations, though.

5 Conclusions

5.1 Methodological Contributions

The approach developed in paper I illustrates how conclusions and decisions based on a population viability analysis could be dangerously misleading if uncertainties are not taken into account. Statements about the viability of a population should be based on the full probability distribution of the stochastic growth rate, and not only on its mode or mean. This is the first time the probabilistic long-term growth rate parameter, $\log \lambda_S$, is estimated (2.1.2). This approach is especially useful in the viability analysis of natural populations experiencing environmental variability.

Paper II mainly stresses that ignoring relevant uncertainty sources generally gives an unwarranted impression of confidence in results. The influence of different uncertainty sources on the statements about the population development has, to our knowledge, never been disentangled (2.1.4). The procedure used in this work increased our understanding of the relative importance of different uncertainty sources, and helps choosing which sources to include when conducting studies on, for example, the impact of climate change

The method developed in paper III allowed us to estimate colonization rates of non-equilibrium metapopulations (2.1.6). Especially for rare species, colonization rates –and conservation decisions based on these– may give misleading conclusions if this approach is not used. We illustrate how the choice of a modelling approach has important implications on metapopulation viability analysis. In this case, we show how a model provides a better description of the process there is no room for model averaging. The modelling approach presented in this study is applicable to other organisms whose metapopulation dynamics are not at equilibrium with the landscape dynamics.

5.2 Implications for Conservation

The Epixylic Moss Study System

The population dynamics of the studied epixylic moss are mainly driven by regional weather fluctuations, i.e. temporal dynamics of habitat quantity and population abundance is less important (2.1.1). However, we do not neglect the importance of local population dynamics and resource levels (variation in dead wood amount). The results also brought light into the species life cycle, supporting the hypothesis that *B. viridis*' spore germination and fertilization can occur within one year after the spore release. However, spore rain from outside the study plots is not discarded; hence, the preceding year's local abundance is not the only spore source.

This is, to our knowledge, the first estimate of a decline of a bryophyte species based on time series data. The model suggests –with a confidence of 81%– that the population will decline in the long term under environmental conditions similar to current conditions (2.1.2). A change in the balance between climatic variables may lead to a further decline of the species, as simulated in paper II. There is a clear risk for a large decline of the *B. viridis* population under all the greenhouse gas emission (SRES) scenarios investigated (2.1.5). The projected decline in *B. viridis* abundance may reflect a decline in many additional similar species, which are sensitive to changes in moisture conditions. Even with this future prospect, a change in greenhouse gas emission policies and the social awareness contemplated by SRES B1 will help to ameliorate the negative effects of anthropogenic climate change on this and many other species.

The Epiphytic Lichens Study System

Given the severe fragmentation of the landscape in the last 150 years, protected areas may only serve as temporary refugia for the species, if connectivity is not otherwise enhanced. Increasing occupancies obtained with retention actions are promising. However, forest retention actions are only one of the possible complementary conservation strategies available that can be articulated with forestry activities. Simulations show, that there is a need to promptly regulate forestry activities with more and stronger complementary conservation strategies –e.g. retention patches, extended rotation– (2.1.7), and that these also need to be evaluated as potential CBD targets. Habitat restoration could also be taken into account to reverse the process of habitat loss and fragmentation (Hanski *et al.*, 1996; Rey Benayas *et al.*, 2009; Convention on Biological Diversity, 2010).

References

Ågren, J., Ehrlén, J. & Solbreck, C. (2008). Spatio-temporal variation in fruit production and seed predation in a perennial herb influenced by habitat quality and population size. *Journal of Ecology* 96(2), 334–345.

Akçakaya, H. R. (2000). Population viability analyses with demographically and spatially structured models. *Ecological Bulletins* 48, 23–38.

Akçakaya, H. R. & Sjögren-Gulve, P. (2000). Population viability analyses in conservation planning: an overview. *Ecological Bulletins* 48, 9–21.

Araújo, M. B., Whittaker, R. J., Ladle, R. J. & Erhard, M. (2005). Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology and Biogeography* 14(6), 529–538.

Bakker, V. J., Doak, D. F., Roemer, G. W., Garcelon, D. K., Coonan, T. J., Morrison, S. A., Lynch, C., Ralls, K. & Shaw, R. (2009). Incorporating ecological drivers and uncertainty into a demographic population viability analysis for the island fox. *Ecological Monographs* 79(1), 77–108.

Bayes, T. & Price, R. (1763). An essay towards solving a problem in the doctrine of chances. *Philosophical Transactions of the Royal Society* 53, 370–418.

Beissinger, S. R. & McCullough, D. R. (2002). *Population viability analysis*. Chicago, USA: University of Chicago Press.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (*in press*). Impacts of climate change on the future of biodiversity. *Ecology Letters*.

Berger, J. O. & Berry, D. A. (1988). Statistical analysis and the illusion of objectivity. *American Scientist* 76(2), 159–165.

Box, G. E. P. (1976). Science and statistics. *Journal of the American Statistical Association* 71(356), 791–799.

Brook, B. W., Burgman, M. A., Akçakaya, H. R., O'Grady, J. J. & Frankham, R. (2002). Critiques of PVA ask the wrong questions: throwing the heuristic baby out with the numerical bath water. *Conservation Biology* 16(1), 262–263.

Brook, B. W., O'Grady, J. J., Chapman, A. P., Burgman, M. A., Akçakaya, H. R. & Frankham, R. (2000). Predictive accuracy of population viability analysis in conservation biology. *Nature* 404(6776), 385–387.

Bull, J. C. & Bonsall, M. B. (2008). Overcompensatory population dynamic responses to environmental stochasticity. *Journal of Animal Ecology* 77(6), 1296–1305.

Burnham, K. P. & Anderson, D. R. (2002). *Model selection and multimodel inference*. Forts Collins, USA: Springer.

Buser, C., Künsch, H., Lüthi, D., Wild, M. & Schär, C. (2009). Bayesian multi-model projection of climate: bias assumptions and interannual variability. *Climate Dynamics* 33(6), 849–868.

Caswell, H. (2001). *Matrix population models: construction, analysis, and interpretation. Sinauer Associates*. 2nd. ed. Sunderland, Massachusetts, USA: Sinauer Associates.

Christensen, J. H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R. K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L. O., Menéndez, C. G., Räisänen, J., Sarr, A. & Whetton, P. (2007). Regional climate projections. In: Solomon, S., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., & Miller, H. L. (Eds.) *Climate Change 2007: The Physical Science Basis*. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press. (Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change).

Clark, J. S. (2005). Why environmental scientists are becoming Bayesians. *Ecology Letters* 8(1), 2–14.

Clark, J. S. & Bjørnstad, O. N. (2004). Population time series: process variability, observation errors, missing values, lags, and hidden states. *Ecology* 85(11), 3140–3150.

Clark, J. S., Carpenter, S. R., Barber, M., Collins, S., Dobson, A., Foley, J. A., Lodge, D. M., Pascual, M., Pielke, R., Pizer, W., Pringle, C., Reid, W. V., Rose, K. A., Sala, O., Schlesinger, W. H., Wall, D. H. & Wear, D. (2001). Ecological forecasts: an emerging imperative. *Science* 293(5530), 657–660.

Clark, J. S., Lewis, M., McLachlan, J. S. & HilleRisLambers, J. (2003). Estimating population spread: what can we forecast well? *Ecology* 84(8), 1979–1988.

Collins, M., Booth, B. B. B., Harris, G. R., Murphy, J. M., Sexton, D. M. H. & Webb, M. J. (2006). Towards quantifying uncertainty in transient climate change. *Climate Dynamics* 27(2-3), 127–147.

Convention on Biological Diversity (2010). *Decision X/2: the strategic plan for biodiversity 2011-2020 and the Aichi biodiversity targets. UNEP/CBD/COP/DEC/X/2*.

Coulson, T., Ezard, T. H. G., Pelletier, F., Tavecchia, G., Stenseth, N. C., Childs, D. Z., Pilkington, J. G., Pemberton, J. M., Kruuk, L. E. B., Clutton-Brock, T. H. & Crawley, M. J. (2008). Estimating the functional form for the density dependence from life history data. *Ecology* 89(6), 1661–1674.

Davison, R., Jacquemyn, H., Adriaens, D., Honnay, O., Kroon, H. de & Tuljapurkar, S. (2010). Demographic effects of extreme weather events on a short-lived calcareous grassland species: stochastic life table response experiments. *Journal of Ecology* 98(2), 255–267.

Déqué, M., Rowell, D. P., Lütji, D., Giorgi, F., Christensen, J. H., Rockel, B., Jacob, D., Kjellström, E., de Castro, M. & van den Hurk, B. (2007). An intercomparison of regional climate simulations for Europe: assessing uncertainties in model projections. *Climatic Change* 81(1), 53–70.

Devenish Nelson, E. S., Harris, S., Soulsbury, C. D., Richards, S. A. & Stephens, P. A. (2010). Uncertainty in population growth rates: determining confidence intervals from point estimates of parameters.(Bersier, L.-F., Ed.) *PLoS ONE* 5(10), e13628.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S. & Mouquet, N. (2010). Defining and measuring ecological specialization. *Journal of Applied Ecology* 47(1), 15–25.

During, H. J. (1979). Life strategies of bryophytes: a preliminary review. *Lindbergia* 5(1), 2–18.

Ellison, A. M. (2004). Bayesian inference in ecology. *Ecology Letters* 7(6), 509–520.

Evans, M. E. K., Holsinger, K. E. & Menges, E. S. (2010). Fire, vital rates, and population viability: a hierarchical Bayesian analysis of the endangered Florida scrub mint. *Ecological Monographs* 80(4), 627–649.

Evju, M., Halvorsen, R., Rydgren, K., Austrheim, G. & Mysterud, A. (2010). Interactions between local climate and grazing determine the population dynamics of the small herb *Viola biflora*. *Oecologia* 163(4), 921–933.

Fazey, I., Fischer, J. & Lindenmayer, D. B. (2005). What do conservation biologists publish? *Biological Conservation* 124(1), 63–73.

Fedrowitz, K., Kuusinen, M. & Snall, T. (2012). Metapopulation dynamics and future persistence of epiphytic cyanolichens in a European boreal forest ecosystem. *Journal of Applied Ecology* 49(2), 493–502.

Fernández-Chacón, A., Bertolero, A., Amengual, A., Tavecchia, G., Homar, V. & Oro, D. (2011). Spatial heterogeneity in the effects of climate change on the population dynamics of a Mediterranean tortoise. *Global Change Biology* 17(10), 3075–3088.

Fowler, H. J., Blenkinsop, S. & Tebaldi, C. (2007). Linking climate change modelling to impacts studies: recent advances in downscaling techniques for hydrological modelling. *International Journal of Climatology* 27(12), 1547–1578.

Fritz, Ö., Gustafsson, L. & Larsson, K. (2008). Does forest continuity matter in conservation? - A study of epiphytic lichens and bryophytes in beech forests of southern Sweden. *Biological Conservation* 141(3), 655–668.

Fritz, Ö., Niklasson, M. & Churski, M. (2009). Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied Vegetation Science* 12(1), 93–106.

Gärdenfors, U. (Ed.) (2010). *Rödlistade arter i Sverige 2010 = The 2010 red list of Swedish species*. Uppsala, Sweden: Swedish Species Information Centre in cooperation with Swedish Environmental Protection Agency.

Gelman, A., Carlin, J. B., Stern, H. S. & Rubin, D. B. (2004). *Bayesian data analysis*. New York: Chapman & Hall / CRC Press.

Gelman, A. & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press Cambridge.

Gignac, L. D. (2001). Bryophytes as indicators of climate change. *The Bryologist* 104(3), 410–420.

Gillespie, G. R., Scroggie, M. P., Roberts, J. D., Cogger, H. G., Mahony, M. J. & McDonald, K. R. (2011). The influence of uncertainty on conservation assessments: Australian frogs as a case study. *Biological Conservation* 144(5), 1516–1525.

Gjerde, I., Blom, H. H., Lindblom, L., Sætersdal, M. & Schei, F. H. (*in press*). Community assembly in epiphytic lichens in early stages of colonization. *Ecology*.

González-Suarez, M., McCluney, K. E., Aurioles, D. & Gerber, L. R. (2006). Incorporating uncertainty in spatial structure for viability predictions: a case study of California sea lions (Zalophus californianus californianus). *Animal Conservation* 9(2), 219–227.

Goodman, D. (2002). Predictive Bayesian population viability analysis: a logic listing criteria, delisting criteria, and recovery plans. *Population viability analysis*. pp 447–469. Chicago, USA: University of Chicago Press.

Gotelli, N. J. & Ellison, A. M. (2006). Forecasting extinction risk with nonstationary matrix models. *Ecological Applications* 16(1), 51–61.

Götmark, F. & Thorell, M. (2003). Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in southern Sweden. *Biodiversity and Conservation* 12(6), 1271–1285.

Granath, G., Strengbom, J. & Rydin, H. (2012). Direct physiological effects of nitrogen on Sphagnum: a greenhouse experiment. *Functional Ecology* 26(2), 353–364.

Hancock, J. A. & Brassard, G. R. (1974). Phenology, sporophyte production, and life history of *Buxbaumia aphylla* in Newfoundland, Canada. *The Bryologist* 77(4), 501–513.

Hanski, I. (1999). *Metapopulation ecology*. Oxford: Oxford University Press. (Oxford Series in Ecology and Evolution).

Hanski, I. (2011). Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *AMBIO* 40(3), 248–255.

Hanski, I. & Gaggiotti, O. E. (2004). *Ecology, genetics, and evolution of metapopulations*. Elsevier Academic Press.

Hanski, I., Moilanen, A. & Gyllenberg, M. (1996). Minimum viable metapopulation size. *The American Naturalist* 147(4), 527–541.

Hanski, I. & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature* 404(6779), 755–758.

Hanski, I. & Ovaskainen, O. (2002). Extinction debt at extinction threshold. *Conservation Biology* 16(3), 666–673.

Hedenås, H. & Ericson, L. (2000). Epiphytic macrolichens as conservation indicators: successional sequence in *Populus tremula* stands. *Biological Conservation* 93(1), 43–53.

Herben, T., Münzbergová, Z., Mildén, M., Ehrlen, J., Cousins, S. a. O. & Eriksson, O. (2006). Long-term spatial dynamics of *Succisa pratensis* in a changing rural landscape: linking dynamical modelling with historical maps. *Journal of Ecology* 94(1), 131–143.

Higgins, S. I., Clark, J. S., Nathan, R., Hovestadt, T., Schurr, F., Fragoso, J. M. V., Aguiar, M. R., Ribbens, E. & Lavorel, S. (2003). Forecasting plant migration rates: managing uncertainty for risk assessment. *Journal of Ecology* 91(3), 341–347.

Hodgson, J. A., Moilanen, A. & Thomas, C. D. (2009). Metapopulation responses to patch connectivity and quality are masked by successional habitat dynamics. *Ecology* 90(6), 1608–1619.

Høistad, F. & Gjerde, I. (2011). *Lobaria pulmonaria* can produce mature ascospores at an age of less than 15 years. *The Lichenologist* 43(05), 495–497.

Hunter, C. M., Caswell, H., Runge, M. C., Regehr, E. V., Amstrup, S. C. & Stirling, I. (2010). Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology* 91(10), 2883–2897.

Inchausti, P. & Halley, J. (2003). On the relation between temporal variability and persistence time in animal populations. *Journal of Animal Ecology* 72(6), 899–908.

IPCC (2007). *Climate change 2007: impacts, adaptation and vulnerability. Contribution of Working Group II to the fourth Assessment Report of the Intergovernmental Panel on Climate Change*.(Canziani, O. F., Palutikof, J. P., van der Linden, P. J., & Hanson, C. E., Eds.) Cambridge, UK: Cambridge University Press.

Jäkäläniemi, A., Tuomi, J., Siikamäki, P. & Kilpiä, A. (2005). Colonization-extinction and patch dynamics of the perennial riparian plant, *Silene tatarica*. *Journal of Ecology* 93(4), 670–680.

Jeltsch, F., Moloney, K. A., Schurr, F. M., Köchy, M. & Schwager, M. (2008). The state of plant population modelling in light of environmental change. *Perspectives in Plant Ecology, Evolution and Systematics* 9(3-4), 171–189.

Johansson, V., Ranius, T. & Snäll, T. (2012). Epiphyte metapopulation dynamics are explained by life-history, connectivity and patch dynamics. *Ecology* 93, 235–241.

Jongejans, E., Jorritsma-Wienk, L. D., Becker, U., Dostál, P., Mildén, M. & Kroon, H. de (2010). Region versus site variation in the population dynamics of three short-lived perennials. *Journal of Ecology* 98(2), 279–289.

Jonsell, B. (Ed.) (2004). *Flora Nordica. General Volume*. Stockholm: Bergius Foundation & Royal Swedish Academy of Sciences.

Jönsson, A. M., Appelberg, G., Harding, S. & Bärring, L. (2009). Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle. *Global Change Biology* 15(2), 486–499.

Jönsson, A. M. & Bärring, L. (2011). Future climate impact on spruce bark beetle life-cycle in relation to uncertainties in regional climate model data ensembles. *Tellus A* 63(1), 158–173.

Jonsson, B. G., Kruys, N. & Ranius, T. (2005). Ecology of species living on dead wood – lessons for dead wood management. *Silva Fennica* 39(2), 289–309.

Keeling, M. J., Brooks, S. P. & Gilligan, C. A. (2004). Using conservation of pattern to estimate spatial parameters from a single snapshot. *Proceedings of the National Academy of Sciences of the United States of America* 101(24), 9155 –9160.

Keith, D. A., Akçakaya, H. R., Thuiller, W., Midgley, G. F., Pearson, R. G., Phillips, S. J., Regan, H. M., Araújo, M. B. & Rebelo, T. G. (2008). Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* 4(5), 560–563.

Kjellström, E., Bärring, L., Gollvik, S., Hansson, U., Jones, C. G., Samuelsson, P., Rummukainen, M., Ullerstig, A., Willén, U. & Wyser, K. (2005). *A 140-year simulation of European climate with the new version of the Rossby Centre Regional Atmospheric Climate Model (RCA3)*. Norrköping, Sweden: Swedish Metereological and Hydrological Institute. (Reports Meteorology and Climatology; 108).

Kjellström, E., Nikulin, G., Hansson, U., Strandberg, G. & Ullerstig, A. (2011). 21st century changes in the European climate: uncertainties derived from an ensemble of regional climate model simulations. *Tellus A* 63(1), 24–40.

Knutti, R. (2010). The end of model democracy? *Climatic Change* 102(3-4), 395–404.

Lättman, H., Lindblom, L., Mattsson, J.-E., Milberg, P., Skage, M. & Ekman, S. (2009). Estimating the dispersal capacity of the rare lichen *Cliostomum corrugatum*. *Biological Conservation* 142(8), 1870–1878.

Lawler, J. J., Aukema, J. E., Grant, J. B., Halpern, B. S., Kareiva, P., Nelson, C. R., Ohleth, K., Olden, J. D., Schlaepfer, M. A., Silliman, B. R. & Zaradic, P. (2006). Conservation science: a 20-year report card. *Frontiers in Ecology and the Environment* 4(9), 473–480.

Lewontin, R. C. & Cohen, D. (1969). On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences of the United States of America* 62(4), 1056–1060.

Lima, M., Julliard, R., Stenseth, N. C. & Jaksic, F. M. (2001). Demographic dynamics of a neotropical small rodent (*Phyllotis darwini*): feedback structure, predation and climatic factors. *Journal of Animal Ecology* 70(5), 761–775.

Löbel, S. & Rydin, H. (2009). Dispersal and life history strategies in epiphyte metacommunities: alternative solutions to survival in patchy, dynamic landscapes. *Oecologia* 161(3), 569–579.

Loehle, C. (2011). Criteria for assessing climate change impacts on ecosystems. *Ecology and Evolution* 1(1), 63–72.

Margules, C. R. & Pressey, R. L. (2000). Systematic conservation planning. *Nature* 405(6783), 243–253.

McClintock, B. T., Nichols, J. D., Bailey, L. L., MacKenzie, D. I., Kendall, W. L. & Franklin, A. B. (2010). Seeking a second opinion: uncertainty in disease ecology. *Ecology Letters* 13(6), 659–674.

Moilanen, A. (2000). The equilibrium assumption in estimating the parameters of metapopulation models. *Journal of Animal Ecology* 69(1), 143–153.

Morris, W. F. & Doak, D. F. (2002). *Quantitative conservation biology: theory and practice of population viability analysis*. Sinauer Associates.

Morris, W. F., Pfister, C. A., Tuljapurkar, S., Haridas, C. V., Boggs, C. L., Boyce, M. S., Bruna, E. M., Church, D. R., Coulson, T., Doak, D. F., Forsyth, S., Gaillard, J.-M., Horvitz, C. C., Kalisz, S., Kendall, B. E., Knight, T. M., Lee, C. T. & Menges, E. S. (2008). Longevity can buffer plant and animal populations against changing climatic variability. *Ecology* 89(1), 19–25.

Muñoz, J., Felicisimo, A. M., Cabezas, F., Burgaz, A. R. & Martinez, I. (2004). Wind as a long-distance dispersal vehicle in the southern hemisphere. *Science* 304(5674), 1144–1147.

Münzbergová, Z., Mildén, M., Ehrlén, J. & Herben, T. (2005). Population viability and reintroduction strategies: a spatially explicit landscape-level approach. *Ecological Applications* 15(4), 1377–1386.

Nakićenović, N. & Swart, R. (2000). *Special Report of the Intergovernmental Panel on Climatic Change (IPCC) on Emissions Scenarios (SRES)*. Cambridge, UK.: Cambridge University Press.

Nikulin, G., Kjellström, E., Hansson, U., Strandberg, G. & Ullerstig, A. (2011). Evaluation and future projections of temperature, precipitation and wind extremes over Europe in an ensemble of regional climate simulations. *Tellus A* 63(1), 41–55.

Nilsson, S. G., Arup, U., Baranowski, R. & Ekman, S. (1995). Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology* 9(5), 1208–1215.

Nitare, J. (Ed.) (2000). *Indicator species for assessing the nature conservation value of woodland sites: a flora of selected cryptogams*. Jönköping: Skogsstyrelsen Förlag.

Nordén, B. & Appelqvist, T. (2001). Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation* 10(5), 779–791.

Noss, R. F. (1983). A regional landscape approach to maintain diversity. *BioScience* 33(11), 700–706.

Öckinger, E., Niklasson, M. & Nilsson, S. G. (2005). Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capacity or habitat quality? *Biodiversity and Conservation* 14(3), 759–773.

Öckinger, E. & Nilsson, S. G. (2010). Local population extinction and vitality of an epiphytic lichen in fragmented old-growth forest. *Ecology* 91(7), 2100–2109.

Økland, T., Bakkestuen, V., Økland, R. H. & Eilertsen, O. (2009). Changes in forest understorey vegetation in Norway related to long-term soil acidification and climatic change. *Journal of Vegetation Science* 15(4), 437–448.

Olds, A. D., Connolly, R. M., Pitt, K. A. & Maxwell, P. S. (2012). Habitat connectivity improves reserve performance. *Conservation Letters* 5(1), 56–63.

Ovaskainen, O. (2002). Long-term persistence of species and the SLOSS problem. *Journal of Theoretical Biology* 218(4), 419–433.

Ovaskainen, O. & Cornell, S. J. (2006). Space and stochasticity in population dynamics. *Proceedings of the National Academy of Sciences* 103(34), 12781–12786.

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37(1), 637–669.

Peters, R. (1997). *Beech forests*. Dordrecht, Netherlands: Kluwer Academic Publishers. (Geobotany).

Popper, S. K. R. (1963). *Conjectures and refutations: the growth of scientific knowledge*. Routledge & K. Paul.

Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M. & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology & Evolution* 22(11), 583–592.

Primack, R. B. (2010). *Essentials of Conservation Biology*. Sinauer Associates.

Randall, D. A., Wood, R. A., Bony, S., Colman, R., Fichefet, T., Fyfe, J., Kattsov, V., Pitman, A., Shukla, J. & Srinivasan, J. (2007). Climate models and their evaluation. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M., & Miller, H. L. (Eds.) *Climate change 2007: The physical science basis, contribution of Working Group I to the fourth Assessment Report of the Intergovernmental Panel on Climate Change*. pp 589–662. Cambridge, United Kingdom and New York, NY, USA: Cambridge University Press.

Rey Benayas, J. M., Newton, A. C., Diaz, A. & Bullock, J. M. (2009). Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. *Science* 325(5944), 1121–1124.

Royama, T. (1992). *Analytical population dynamics*. London: Chapman and Hall.

Samuelsson, P., Jones, C. G., Willén, U., Ullerstig, A., Gollvik, S., Hansson, U., Jansson, C., Kjellström, E., Nikulin, G. & Wyser, K. (2011). The Rossby Centre Regional Climate Model RCA3: model description and performance. *Tellus A* 63(1), 4–23.

Snäll, T., Benestad, R. E. & Stenseth, N. C. (2009). Expected future plague levels in a wildlife host under different scenarios of climate change. *Global Change Biology* 15(2), 500–507.

Snäll, T., Hagström, A., Rudolphi, J. & Rydin, H. (2004). Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales - importance of past landscape structure, connectivity and local conditions. *Ecography* 27(6), 757–766.

Snäll, T., O´Hara, R. B., Ray, C. & Collinge, S. K. (2008). Climate-driven spatial dynamics of plague among prairie dog colonies. *American Naturalist* 171(2), 238–248.

Snäll, T., Pennanen, J., Kivisto, L. & Hanski, I. (2005). Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. *Oikos* 109(2), 209–222.

Snäll, T., Ribeiro, P. J. & Rydin, H. (2003). Spatial occurrence and colonisations in patch-tracking metapopulations: Local conditions versus dispersal. *Oikos* 103(3), 566–578.

Spiegelhalter, D. J., Best, N. G., Carlin, B. P. & Linde, A. van der (2002). Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society. Series B (Statistical Methodology)* 64(4), 583–639.

Stenseth, N. C. (1999). Population cycles in voles and lemmings: density dependence and phase dependence in a stochastic world. *Oikos* 87(3), 427–461.

Stenseth, N. C., Chan, K.-S., Tavecchia, G., Coulson, T., Mysterud, A., Clutton-Brock, T. & Grenfell, B. (2004). Modelling non-additive and nonlinear signals from climatic noise in ecological time series: Soay sheep as an example. *Proceedings of the Royal Society B: Biological Sciences* 271(1552), 1985–1993.

Stenseth, N. C., Mysterud, A., Ottersen, G., Hurrell, J. W., Chan, K.-S. & Lima, M. (2002). Ecological effects of climate fluctuations. *Science* 297(5585), 1292–1296.

Tebaldi, C. & Knutti, R. (2007). The use of the multi-model ensemble in probabilistic climate projections. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* 365(1857), 2053 –2075.

Tilman, D., May, R. M., Lehman, C. L. & Novak, M. A. (1994). Habitat destruction and the extinction debt. *Nature* 371(1), 65–66.

Toräng, P., Ehrlén, J. & Ågren, J. (2010). Linking environmental and demographic data to predict future population viability of a perennial herb. *Oecologia* 136(1), 99–109.

Tuljapurkar, S. & Orzack, S. H. (1980). Population dynamics in variable environments I. Long-run growth rates and extinction. *Theoretical Population Biology* 18(3), 314–342.

Turchin, P. & Berryman, A. A. (2000). Detecting cycles and delayed density dependence: a comment on Hunter & Price (1998). *Ecological Entomology* 25(1), 119–121.

Verheyen, K., Vellend, M., Van Calster, H., Peterken, G. & Hermy, M. (2004). Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants. *Ecology* 85(12), 3302–3312.

Wade, P. R. (2002). Bayesian population viability analysis. *Population viability analysis*. pp 213–239. Chicago: The University of Chicago Press.

Werth, S., Wagner, H. H., Gugerli, F., Holderegger, R., Csencsics, D., Kalwij, J. M. & Scheidegger, C. (2006). Quantifying dispersal and establishment limitation in a population of an epiphytic lichen. *Ecology* 87(8), 2037–2046.

Wiklund, K. & Rydin, H. (2004). Ecophysiological constraints on spore establishment in bryophytes. *Functional Ecology* 18(6), 907–913.

Zartman, C. E., Nascimento, H. E. M., Cangani, K. G., Alvarenga, L. D. P. & Snall, T. (*in press*). Fine-scale changes in connectivity affect the metapopulation dynamics of a bryophyte confined to ephemeral patches. *Journal of Ecology* .

Stor Tack! – Muchas Gracias! – Thank you!

I thank God for letting faith and science coexist inside me, two complementary prisms to see the world and seek for the Truth. I'm still far from it, though.

I thank infinitely to Celi, for being my support on this journey, since she encouraged me to submit the application to this PhD, until the very last minute when I submitted this thesis. Estuviste incluso en el campo compartiendo garrapatas conmigo. Gracias Amor! Gracias por estar a mi lado de "este" lado del charco. Gracias por tu "Sí" hace ya más de cinco años. Gracias por hacerme papá. La vida sería tan aburrida sin vos! Te Amo.

Gracias hija por venir a este mundo a llenarnos de felicidad, y a desordenarnos los tuppers y los esquemas. Gracias por tus sesiones de Clariterapia que tanto necesité en este tiempo. Te Amo.

Gracias a mis padres y hermanos: Pá, Má, Pelado, Lili, Ceci, Fede, Seba, Juanjo y Mica. ¡Qué grande y hermosa familia tengo! Gracias por sonreírnos en una computadora cuando lo que querían era tenernos al lado. Sin su apoyo y esfuerzo este viaje hubiese sido una muy muy pesada carga.

I am especially thankful to my main supervisor Tord, for he not only guided and supported me throughout my studies, but he also taught me something every day. Thank you for the time and dedication you spent on my education. Thank you for the helpful comments on this thesis and manuscripts.

I am also thankful to Lena and Thomas, for they have always been there to guide me. Thank you for the helpful comments on this thesis.

I want to thank you Katja for being the perfect office mate. The next person in "my" office would have to work hard to meet the standard this small-big person has set. Also, thank you for the helpful comments that improved this manuscript.

I am very thankful to those that taught me in the field. Niklas Lönel, Karin Wiklund, Mauricio Fuentes, Örjan Fritz and Mats Nicklasson: thank you for the knowledge imparted.

I thank to my co-authors for the enriching experience it was working with you. I hope we had the opportunity to collaborate again in the future.

Thanks to the many friends whose lives happily crossed with mine during these years in Uppsala and enriched my soul. To name YOU ALL would be fortunately too long… so here we go! Sabri, Dani, Valen y el Gran Costantín! Eri, Li y Amanda, Mer, Fer y Martu, Patri y Oscar, Jessi, Gonza y las preciosas, Hernán, Anna-Karin y los enanos, Johan och Johanna, Katja, Sonja, Karin, Nicole, Berrit, Isa, Ra, Bea, Magda y Albert, Martin P, Blas, Victor F, Pato, Annika, Joseph, Rodrigo, Alejandra y flia, Cecilia, Aldo, Siri, Jonas och family, and Jane M.

I thank my colleagues from the department, especially to Sonja, Nicole, Debora, Karin, Astrid, Berrit, Victor, Jens, Mats H. and L., Måns, Camilla, for making me smile and laugh at the corridors, making every day just that bit better.

A mis amigos de siempre. La distancia y el tiempo preserva sólo a los buenos amigos. Gracias por estar luego de tanto tiempo y distancia.

I am thankful to SLU for the enormous amount of resources it allocated on my studies.

This work was funded by Formas.

Uppsala 7, June 2012.